PhD THESIS

Marine Ecology speciality

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ECOLOGIE EN MER DES PHOQUES DE WEDDELL DE L'ANTARCTIQUE DE L'EST EN RELATION AVEC LES PARAMETRES PHYSIQUES DE L'ENVIRONNEMENT

AT SEA ECOLOGY OF WEDDELL SEALS IN EAST ANTARCTICA IN RELATION WITH ENVIRONMENTAL PHYSICAL PARAMETERS

Thesis defended on the 9th of October 2014

In front of the following committee:

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Declaration of originality

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28th of January 2015,

Karine Heerah

A mes merveilleux parents,

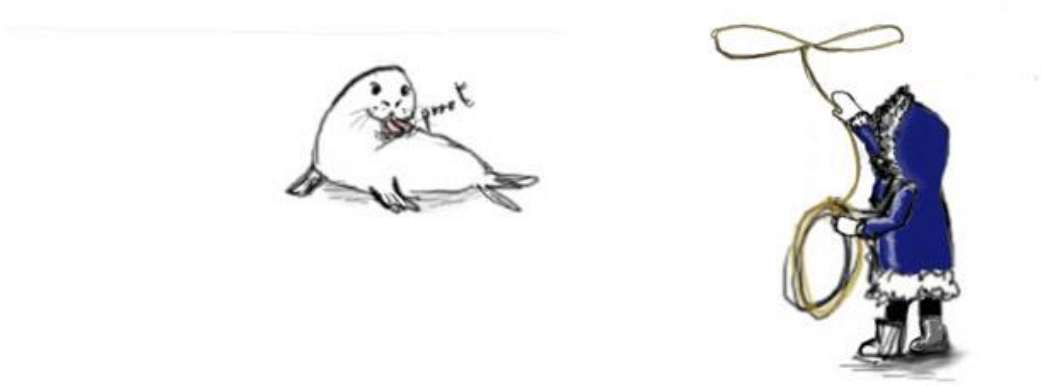
Mon frère et mes sœurs ainsi qu'Henri, Janet,

Et Michèle,

« Pendant que je regarde vers le large, le soleil se couche insensiblement, les teintes bleues si variées et si douces des icebergs sont devenues plus crues, bientôt le bleu foncé des crevasses et des fentes persiste seul, puis graduellement succède avec une douceur exquise une teinte maintenant rose et c'est tellement beau, qu'en me demandant si je rêve, je voudrais rêver toujours…

…On dirait les ruines d'une énorme et magnifique ville tout entière du marbre le plus pur, dominée par un nombre infini d'amphithéâtres et de temples édifiés par de puissants et divins architectes. Le ciel devient une coquille de nacre où s'irisent, en se confondant sans se heurter, toutes les couleurs de la nature… Sans que je m'en aperçoive, la nuit est venue et lorsque Pléneau, en me touchant l'épaule, me réveille en sursaut de cette contemplation, j'essuie pertinemment une larme, non de chagrin, mais de belle et puissante émotion. »

Jean-Baptiste Charcot « Le Français au Pôle Sud »



Dessin de Coralie Chorin

ABSTRACT

The Southern Ocean and more specifically the sea-ice zone supports globally significant ecosystems including abundant populations of marine mammals and seabirds. In the marine environment, resources are heterogeneously distributed and structured in patches driven by physical features of the environment at different spatio-temporal scales. Among the activities included in the habitat use concept, foraging is one of the most important because obtaining adequate food supply is a basic requirement of all other life-history traits. The optimal foraging theory predicts that predators should adjust their movements and behaviour in relation to prey density (in both horizontal and vertical dimensions in the case of marine predators). Thus, studying the movement patterns and diving behaviour of top predators in relation with biotic and abiotic environmental features can provide valuable insights in the behavioural tactics they have evolved and/or learned to maximize prey acquisition in a given environment. This is even more relevant in polar regions where animals face particularly harsh conditions (*e.g.* darkness and associated reduced productivity for most of the year, sea-ice cover, cold water and air, strong winds). The Weddell seal is the only marine mammal inhabiting the coastal fast-ice area year-round. While its behaviour has been well studied in summer when individuals are breeding or moulting on the sea-ice, virtually nothing is known about their winter ecology. However, winter is a crucial period in Weddell seals life cycle during which they spend 80% of their time diving under the ice to store the energy needed for the following breeding season. Using telemetric data, the main aim of this thesis was to improve our understanding of the foraging strategies adopted by Weddell seals during winter in two locations of East Antarctica (Dumont D'Urville and Davis). First, we developed two methods to identify and quantify within dive foraging effort from both high and low-resolution dive datasets. Then, these foraging metrics were used to investigate the influence of several key abiotic parameters of the Antarctic environment on Weddell seals' foraging behaviour. Although Weddell seals from Davis travelled more during winter, overall Weddell seals from both locations essentially remained and foraged in areas close to the coast associated with highly concentrated ice. Our results showed sea-ice concentration did not influence Weddell seals' behaviour. However, the pluri-annual residency of focal seals to similar areas suggested they relied on smaller features within the fast-ice, such as perennial tide cracks close to land. At both locations, seals increased their foraging effort during winter likely responding

to the approach of the pup birth (individuals were mainly females). The seals foraged essentially in shallow waters in areas where the topography is likely inducing upwelling of the nutrient enriched water masses, such as the modified circumpolar deep water in which Weddell seals from DDU increased their foraging effort throughout winter. At both locations, Weddell seals exhibited complex diving behaviour and used both pelagic and benthic strategies, reflecting the opportunistic nature of their feeding. They also adapted their diving behaviour to light intensity suggesting they follow the vertical migration of their prey, such as *P. antarcticum.* Overall, Weddell seals seemed to optimize their foraging strategies during winter by adapting their foraging behaviour in response to physical parameters of their environment (*e.g.* features in the fast-ice, topography and hydrology) that are likely to be associated with better prey availability and accessibility, as well as regular access to breathing sites. At finer scale the foraging behaviour of Weddell seals appear to respond to the distribution and availability of prey in the water column (*i.e.* switching from pelagic to benthic foraging, exhibiting diurnal behaviour, and the complexity of the dives). Our study revealed some key foraging strategies adopted by the Weddell seals demonstrating that they actively optimize their spatial use of the fast-ice environment in both the temporal, horizontal and vertical dimensions during winter.

RESUME

L'Océan Austral, en particulier la zone englacée abritent d'importants écosystèmes incluant d'abondantes populations de mammifères et d'oiseaux marins. Dans l'environnement marin, les ressources sont distribuées de façon hétérogène et structurées en parcelles de proies. Celles-ci dépendent des caractéristiques physiques de l'environnement à différentes échelles spatio-temporelles. De toutes les activités comprises dans le concept d'utilisation de l'habitat, la recherche alimentaire est l'une des plus importantes. En effet, s'approvisionner de manière adéquate est un prérequis nécessaire pour tous les autres traits d'histoire de vie. La théorie optimale de l'approvisionnement prédit qu'un prédateur devrait ajuster ses déplacements et son comportement à la densité de proie (à la fois dans les dimensions horizontales et verticales dans le cas des prédateurs marins). Par conséquent, l'étude des mouvements et du comportement de plongée des prédateurs marins en relation avec les caractéristiques biotiques et abiotiques de l'environnement permet d'apporter des indications précieuses sur les stratégies comportementales innées et/ou qu'ils ont développé afin de maximiser l'acquisition des proies dans un environnement donné. Ceci est encore d'autant plus intéressant dans les régions polaires où les animaux vivent dans des conditions particulièrement difficiles (par exemple, l'obscurité et la baisse de productivité associée pour la majeure partie de l'année, la couverture de glace, l'eau et l'air froid ou des vents forts). Le phoque de Weddell est le seul mammifère marin vivant toute l'année dans la banquise permanente. Bien que son comportement ait été bien étudié en été lorsque les individus se reproduisent et muent sur la glace de mer, nous ne savons presque rien de leur l'écologie hivernale. Cependant, l'hiver est une période cruciale dans le cycle de vie des phoques de Weddell durant laquelle ils passent 80% de leur temps à chasser sous la glace afin de stocker l'énergie nécessaire pour la saison de reproduction suivante. Grâce à l'utilisation de données télémétriques, l'objectif principal de cette thèse était d'améliorer notre compréhension des stratégies de recherche alimentaire adoptées par les phoques de Weddell pendant l'hiver dans deux régions de l'Antarctique de l'Est (Dumont D'Urville et Davis). Tout d'abord, nous avons développé deux méthodes permettant d'identifier et de quantifier l'effort de recherche alimentaire au sein de la plongée, pour des données de plongée haute et basse résolutions. Ces indices de l'effort de recherche alimentaire ont été ensuite utilisés afin d'étudier l'influence de

plusieurs paramètres clés de l'environnement sur le comportement de recherche alimentaire des phoques de Weddell. Bien que les phoques de Weddell de Davis aient parcouru de plus grandes distances pendant l'hiver, les phoques de Weddell des deux localités sont essentiellement restés en zone côtière dans de la glace de mer très concentrée. Nos résultats montrent que la concentration de glace de mer n'influence pas le comportement des phoques de Weddell. Toutefois, l'occupation pluriannuelle des phoques dans les mêmes régions suggèrent qu'ils dépendent de fissures permanentes dans la glace. Dans les deux localités, les phoques ont accru leur effort de recherche alimentaire avec l'avancée de l'hiver, probablement en raison de l'arrivée de la naissance du petit (les individus équipés étant essentiellement des femelles). Les phoques ont concentré leur effort de recherche alimentaire dans des zones peu profondes où la bathymétrie favorise la remontée d'eau enrichie en nutriment, comme par exemple l'eau circumpolaire modifiée. Cette masse d'eau a en effet été majoritairement utilisée par les phoques pendant tout l'hiver. Les phoques de Weddell des deux populations ont révélé des comportements de plongée complexes, avec la capacité de passer d'une stratégie de recherche alimentaire pélagique à benthique. Ceci reflète bien le comportement opportuniste de ces phoques. Par ailleurs, les phoques ont montré qu'ils adaptent leur comportement de plongée à l'intensité lumineuse. Ceci suggère qu'ils suivent les migrations verticales de leur proie, comme par exemple, *P. antarcticum.* De manière générale, les phoques de Weddell semblent optimiser leur stratégie de recherche alimentaire pendant l'hiver en adaptant leurs réponses comportementales à des paramètres physiques de l'environnement (*e.g.* les caractéristiques de la banquise, la topographie et l'hydrologie) susceptibles d'être associés à une meilleure disponibilité et accessibilité des proies et donnant accès à des trous de respiration. A plus fine échelle, les phoques de Weddell semblent ajuster leur comportement à la distribution et la disponibilité des proies dans la colonne d'eau (*e.g.* passage d'une stratégie pélagique à benthique, comportement diurne, complexité des plongées). Notre étude a révélé d'importantes stratégies de recherche alimentaires adoptées par les phoques de Weddell, démontrant qu'ils optimisent de manière active leur utilisation de la zone de banquise permanente pendant l'hiver.

REMERCIEMENTS

Au moment où j'écris ces remerciements de thèse, j'ai réalisé mes deux rêves d'enfants les plus chers : faire une thèse et aller en Antarctique. Je ressors de ces trois années de thèse plus passionnée que jamais et je me sens chanceuse d'avoir pu à la fois travailler sur un jeu de données extraordinaire, faire une co-tutelle, aller sur le terrain et participer à de nombreuses conférences. Enfin et surtout, j'ai eu la chance d'avoir été si bien accompagnée dans mon projet, à la fois professionnellement et personnellement. Ces trois années ont également été ponctuées de nombreuses rencontres fabuleuses aux quatre coins du monde. J'ai été gâtée et j'en suis comblée. Afin de n'oublier personne, je vais faire court et remercier chaleureusement toutes les personnes (et elles se reconnaitront) qui ont contribué de près ou de loin à l'aboutissement de ce projet. Plus particulièrement, MERCI à mes directeurs de thèse Jean-Benoît Charrassin, Mark Hindell et Christophe Guinet, à ma famille, mes amis et Malcolm pour votre soutien inébranlable.

Encore une fois, merci à tous et bonne lecture…

At the time I write these acknowledgements, I have accomplished my childhood dreams: completing my PhD and working in Antarctica. After spending three years working on my PhD I finish more passionate than ever and feel so lucky to have had the chance to work on an extraordinary dataset, be part of a co-tutelle project, travel South for fieldwork and attend many conferences. Finally, and most importantly, I feel really lucky to have been given so much professional and personal support. Over the past three years I have met many fabulous people around the world. I have been spoiled to be given such an amazing opportunity such as this, and feel very accomplished. I would like to warmly thank all the people who contributed to this project in one way or another. Special THANKS must go to my PhD supervisors Jean-Benoît Charrassin, Mark Hindell et Christophe Guinet, to my family, friends and Malcolm for their unwavering support.

Once again, thank you all and enjoy your reading…

En attendant d’autres aventures… While waiting for other adventures…

TABLE OF CONTENTS

PUBLICATIONS & PRESENTATIONS 21

PART I: GENERAL INTRODUCTION 23

A - WINTER ANTARCTIC ENVIRONMENT 24

1. Antarctica and study sites 24
2. Circulation and water masses 28
3. Sea-ice environment 34

B - SEA-ICE DEPENDENT PELAGIC ECOSYSTEM 38

1. Sea-ice community 38
2. Upper trophic levels depending on sea-ice habitat 39

2.1 The Antarctic continental shelf assemblages 40

2.2. The Antarctic shelf-break assemblages 41

C - STUDYING THE FORAGING ECOLOGY OF TOP PREDATORS 43

1. Foraging in a heterogeneous environment 43
2. Detection of foraging behaviour 46

2.1 Inferring foraging activity from tracking data 47

2.2 Direct measurements of foraging success 48

2.3 Inferring foraging activity from diving behaviour 49

3. Habitat use of top predators 50

D - THE WEDDELL SEAL 56

PAPER 1 57

E - CONTEXT, OBJECTIVES AND THESIS OUTLINE 61

PART II : METHODOLOGICAL DEVELOPMENTS 63

A - INTRODUCTION 64

B - PAPER 2 67

1. Abstract 68
2. Introduction 70

3. Materials and methods 74
3.1 Tagging procedure *74*
3.2 Fine scale analysis of foraging behaviour *75*
4. Results 82
4.1 General diving behaviour *82*
4.2 Foraging behaviour *83*
5. Discussion 93
5.1 Detection of intensive foraging activity within dives *93*
5.2 Fine scale foraging strategy of Weddell and southern elephant seal *96*
6. Conclusion 98
7. Acknowledgements 98
8. Appendix 99

C - PAPER 3 101
1. Abstract 102
2. Introduction 104
3. Material and Methods 107
3.1 Fine scale analysis of foraging behaviour *107*
3.2 From high-resolution to low-resolution dive datasets *109*
4. Results 114
4.1 General diving behaviour *114*
4.2 From high-resolution to low-resolution dives: estimation of foraging effort *115*
5. Discussion 119
5.1 Foraging effort in low-resolution dives *119*
5.2 Ecological applications *122*
6. Conclusion 125
7. Aknowledgements 126
8. Appendix 126

D - CONCLUSION 129

PART III: WEDDELL SEALS HABITAT USE DURING ANTARCTIC WINTER 131

A - INTRODUCTION 132

B - PAPER 4 135
1. Abstract 136
2. Introduction 137
3. Materiel and methods 140
3.1 Animal handling and tagging 140
3.2 Data collected from the tags 140
3.3 Argos Kalman filtering 141
3.4 Bathymetry and sea-ice data 142
3.5 Hydrological data 143
3.6 Behavioural data 144
2.7 Statistical analysis 146
4. Results 148
4.1 Tag performance, foraging areas and diving features of Weddell seals in winter 148
4.2 Use of hydrographic environment 152
4.3 Influence of environmental and temporal factors on foraging behaviour 154
4.3.3 Bottom time residuals 157
5. Discussion 158
5.1 Effect of winter advancement and circadian light cycle on diving patterns 159
5.2 Habitat selection and influence of the environment on foraging behaviour 160
5.3 Future studies 164
6. Conclusion 165
7. Ackowledgement 165
8. Appendix 166

C - PAPER 5 169
1. Abstract 170
2. Introduction 172
3. Material and methods 176
3.1 Instrumentation 176
3.2 Argos locations filtering and track simulations 176
3.3. Environmental data 177
3.4 Diving behaviour 179
3.5. Movement pattern analyses 181

3.6 Statistical analysis *183*
4. Results 185
4.1 Tag performance *185*
4.2 Movement patterns *186*
4.3 Diving behaviour *188*
4.4 Identification of Area-restricted search *189*
4.5 Area-restricted search behaviour *193*
5. Discussion 205
5.1 Methodological discussion *205*
5.2 Foraging strategies of the focal Weddell seals *208*
5.3 Habitat use *212*
6. Conclusion 216
7. Acknowledgements 217
8. Appendix 218

D - CONCLUSION 234

PART IV: GENERAL DISCUSSION, CONCLUSIONS AND PERSPECTIVES 237

A - METHODOLOGICAL DISCUSSION 238
1. Analysis of diving behaviour to infer foraging activity 238
1.1 The development of a new method *238*
1.2 Detection and prediction of foraging success *240*
2. Track analysis and implementation of the foraging effort index 242

B - ECOLOGY OF THE WEDDELL SEAL DURING WINTER 246
1. Context 246
2. The fast-ice: a primary habitat for Weddell seals 247
2.1 Movement patterns of Weddell seals during winter *247*
2.2 Overwintering in fast-ice allows predator and inter-specific competition avoidance *248*
2.3 Assessment of important sea-ice features to Weddell seals *249*
3. Foraging strategies of Weddell seals 251
3.1 Optimal foraging from a breathing hole *252*
3.2 Inference on Weddell seals' diet from diving behaviour *253*

3.3. Weddell seals' adaptation to winter conditions 256

3.4 Environmental parameters influencing the behaviour of Weddell seals 258

C – CONCLUSION AND PERSPECTIVES 261

1. Main conclusions 261

2. Climate change and Weddell seals 262

2.1 Observed changes in Antarctic sea-ice 262

2.2 Assessment of potential climate change effects on Weddell seals 263

3. Perspectives 265

3.1 Information on prey: the missing link between top predators and their environment 265

3.2 Improving our understanding of climate variability effects on Weddell seals 266

REFERENCES 269

APPENDIX 293

APPENDIX A 294

APPENDIX B – SCRIPT S2.1 OF PAPER 2 297

PUBLICATIONS & PRESENTATIONS

Publications produced as part of this thesis

Paper 1 – Part I: Heerah K., Charrassin J.-B. Le Phoque de Weddell (2 p., ***In press***). Atlas des mammifères marins de France et d'Outre Mer, Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris.

Paper 2 – Part II: Heerah K., Hindell M., Guinet C. and Charrassin J.B. A new method to quantify within dive foraging behaviour in marine predators (**2014**). **PlosONE**

Paper 4 – Part III: Heerah K., Andrews-Goff V., Williams G., Sultan E., Hindell M., Patterson T. and Charrassin J.B. Ecology of Weddell seals during winter: influence of hydrographic parameters on their foraging behaviour (**2013**). **Deep Sea Research II** 88 (89): 23-33.

Intent to submit publications as part of this thesis

Paper 3 – Part II: Heerah K., Hindell M., Guinet C. and Charrassin J.B. From high resolution to low resolution dive datasets: a new index to quantify the foraging effort of marine predators (***Under revision*** in **Animal Biotelemetry**, proceedings of Biologging V).

Paper 5 – Part III: Heerah K., Hindell M.A., Roquet F., Andrews-Goff V., Field I., McMahon C. and Charrassin J.B. (***In prep***). Where to forage? Contrasting behaviours between two colonies of Weddell seals in East Antarctica.

Other publications

Koubbi P., Hosie G., Constable A., Raymond B., Moteki M., Améziane N., Causse R., Fuentes V., **Heerah K.**, Penot F., Vincent D., Ancel A., Bost C.A., Eléaume M., Lindsay D., Lindsay M., Cottin M., Charrassin J.B., Ropert-Coudert Y., Toda R., Grossmann M., Hopcroft R., Ozouf-Costaz C., Zimmer I. and CEAMARC experts. Estimating the biodiversity of the shelf and oceanic zone of the d'Urville Sea (East Antarctica) for eco-regionalisation using the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys (2011). Report to the CCAMLR workshop on Marine Protected Areas. Brest, France –2011.

Labrousse S., VacquiéGarciaJ. , **Heerah K.**, Bailleul F., Guinet C., Hindell M.A., Charrassin J.B. (*Under revision* in Progress in Oceanography). What are southern elephant seals looking for? Long trip from Kerguelen to the Antarctic zone: The length and breadth of the mystery.

Presentations

Heerah K., Hindell M., Guinet C. and Charrassin J.B. A new method to quantify within dive foraging behaviour in marine predators. Poster. 20th biennial conference on marine mammals, Otago University, Dunedin, New-Zealand – 2013. **Awarded poster.**

Heerah K., Hindell M., Guinet C. and Charrassin J.B. A new method to quantify within dive foraging behaviour in marine predators. **Oral presentation.** SCAR (Scientific Committee on Antarctic Research) Biology Open Science Conference. Barcelona – 2013.

Heerah K., Andrews-Goff V., Williams G., Sultan E., Hindell M. and Charrassin J.B. Ecology of Weddell seals during winter: influence of environmental parameters on their foraging behaviour. **Oral presentation.** SCAR (Scientific Committee on Antarctic Research) Open Science Conference. Portland – 2012.

Heerah K., Ancel A., Bost C.A., Zimmer I., Charrassin J.B. Distribution areas of top predators in the D'Urville sea during summer and winter. **Oral presentation.** CCAMLR Workshop on Marine Protected Areas. Brest, France –2011.

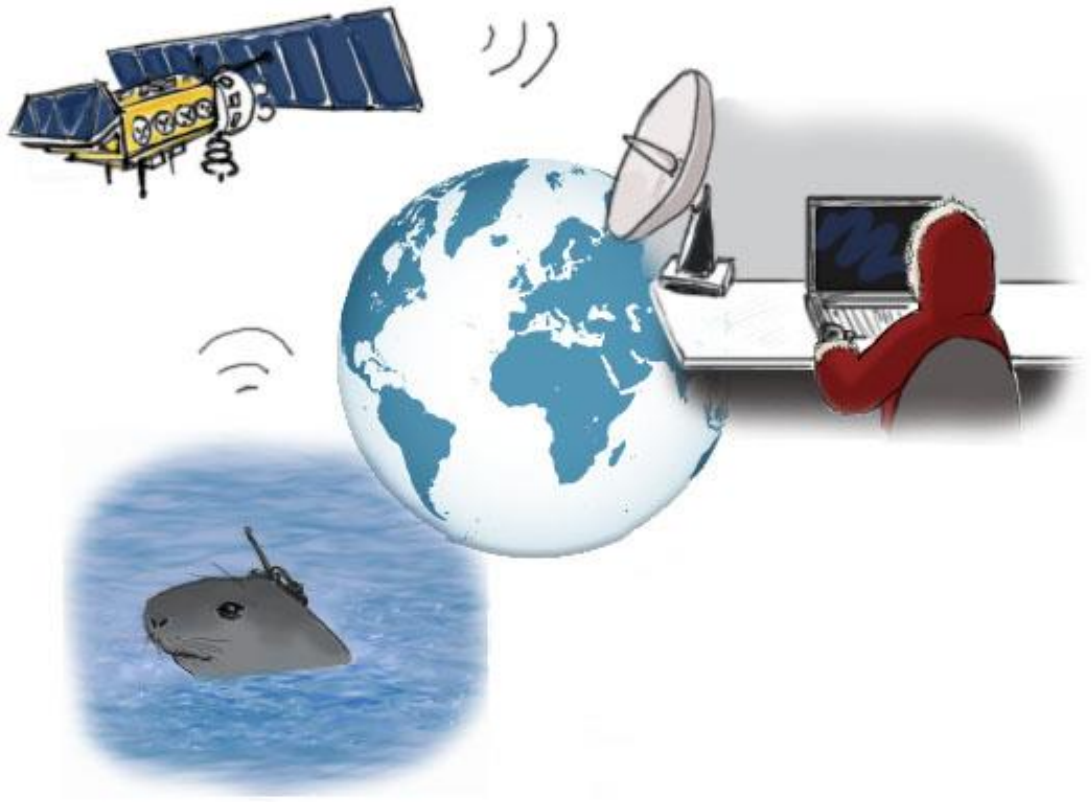
Heerah K., Andrews-Goff V., Williams G., Sultan E., Hindell M. and Charrassin J.B. Ecology of Weddell seals during winter: influence of hydrographic parameters on their foraging behaviour. **Oral presentation.** CNFRA (French National Committee on Antarctic and Arctic Research) scientific conference. Paris – 2011.

Heerah K., Andrews-Goff V., Williams G., Sultan E., Hindell M. and Charrassin J.B. Ecology of Weddell seals during winter: influence of ocean and sea ice parameters on their foraging behaviour. **Poster** for 4th biologging conference. Hobart– 2011.

Heerah K., Andrews-Goff V., Williams G., Sultan E., Hindell M. and Charrassin J.B. Ecology of Weddell seals during winter: influence of hydrographical parameters on their foraging behaviour. **Poster** for the SCAR Open Science Conference. Buenos Aires – 2010.

PART I

GENERAL INTRODUCTION



Dessin de Coralie Chorin

A - Winter Antarctic environment

1. Antarctica and study sites

Antarctica is Earth's southernmost continent and contains the geographic South Pole (Fig. 1.1). It is the fifth largest continent with a surface area of 14 million km². The Antarctic continent is surrounded by the Southern Ocean which spreads over 77 million km², thus representing ~ 22% of the global ocean. The Southern Ocean itself is composed of three broad-scale deep depressions: the Weddell-Enderby, Bellingshausen-Amundsen and the Australian-Antarctic basin (Fig. 1.1). The latter corresponds to the East-Antarctic region and is bounded to the west by the Kerguelen plateau and to the north and east by the south-east Indian mid-ocean ridge. This basin is not entirely closed, and important depressions allow exchanges of basin water masses with those to the east and west (Nicol *et al.* 2010). In contrast to other Antarctic regions, the Indian and Pacific sectors between 80 and 160°E are characterized by a relatively uniform coastline unbroken by major geographic features (Nicol *et al.* 2010). This region is contained within the CCAMLR (the Commission for the Conservation of Antarctic Marine Living Resources) Statistical division 58.4.1 and includes several sites of Antarctic Bottom Water formation (see section "circulation and water masses") (Nicol et al., 2000). These characteristics highlight the importance of the East Antarctic region both from a biological and an oceanographic perspective. Moreover, both coastal and offshore physical features of this region influence the oceanography and associated biology which exhibit regional variations (Nicol et al., 2000).

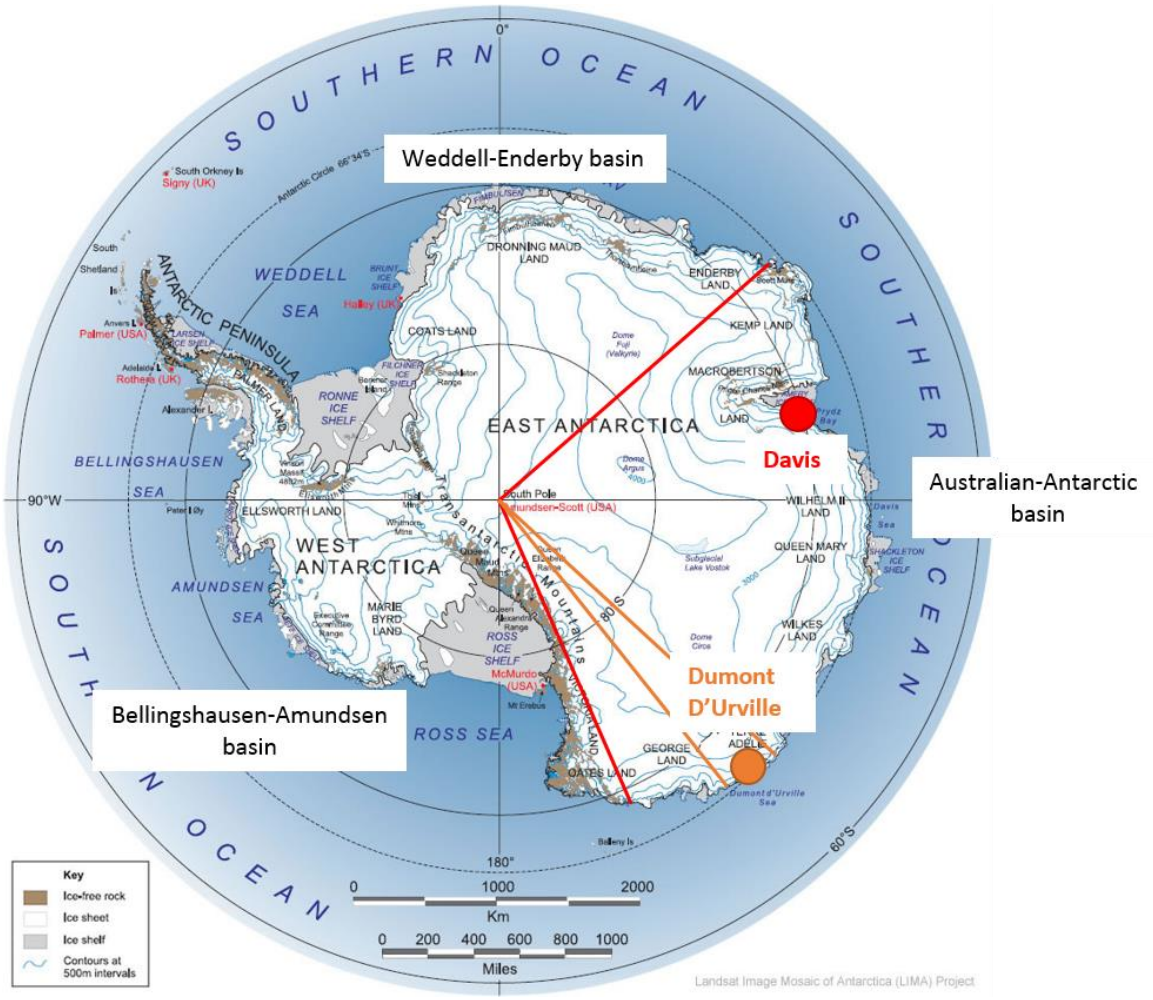


Figure 1.1. Map of the Antarctic continent and the Southern Ocean. The red lines bound the Antarctic region and the Australian claims. The orange lines bound the French claim.

This PhD focused on two populations of Weddell seals from two different locations of East Antarctica located at the opposite frontiers of the 80-160°E sector: Davis and Dumont d'Urville (DDU) (Fig. 1.1). The Davis site (~67°S 78°E) is located at the western edge of the focal area in a bay (*i.e.* Prydz Bay) characterized by a broad basin (*i.e* the Amery depression), which main features include two elongated deep channels, deep small depressions and two offshore banks (Fig. 1.2a). The Svenner channel is a deep trough parallel to the Davis coastline while the Prydz Channel runs along the western edge of the Amery depression, extending to the continental shelf edge. Offshore from the Amery depressions the shelf shallows to form the Four Ladies bank on the eastern side of the Prydz channel and the Fram bank on its western side (O'brien & Leitchenkov 1997) (Fig. 1.2a). In contrast, DDU (66°40'S 140°E) is located at the eastern edge of East Antarctica where the Antarctic continental shelf between 138°E and 147°E (including DDU) is narrower than in Davis and marked by two deep regions and two plateaux (Beaman *et al.* 2011) (Fig. 1.2b). To the west, there is the deep D'Urville trough which extends from the coast at 141°E to the northwest extending to the continental shelf edge. To the east, the Adelie depression is isolated from the Australian-Antarctic Basin by the shallow Adelie sill. Between the D'Urville trough and the Adelie depression, the shallow Adélie bank connects the coast to the shelf break. To the northeast there is the Mertz bank (Beaman *et al.* 2011) (Fig. 1.2b). The bathymetric features of these regions play a crucial role on the hydrological circulation over the Antarctic shelf which, in combination with sea-ice conditions, will in turn affect the productivity of the areas.

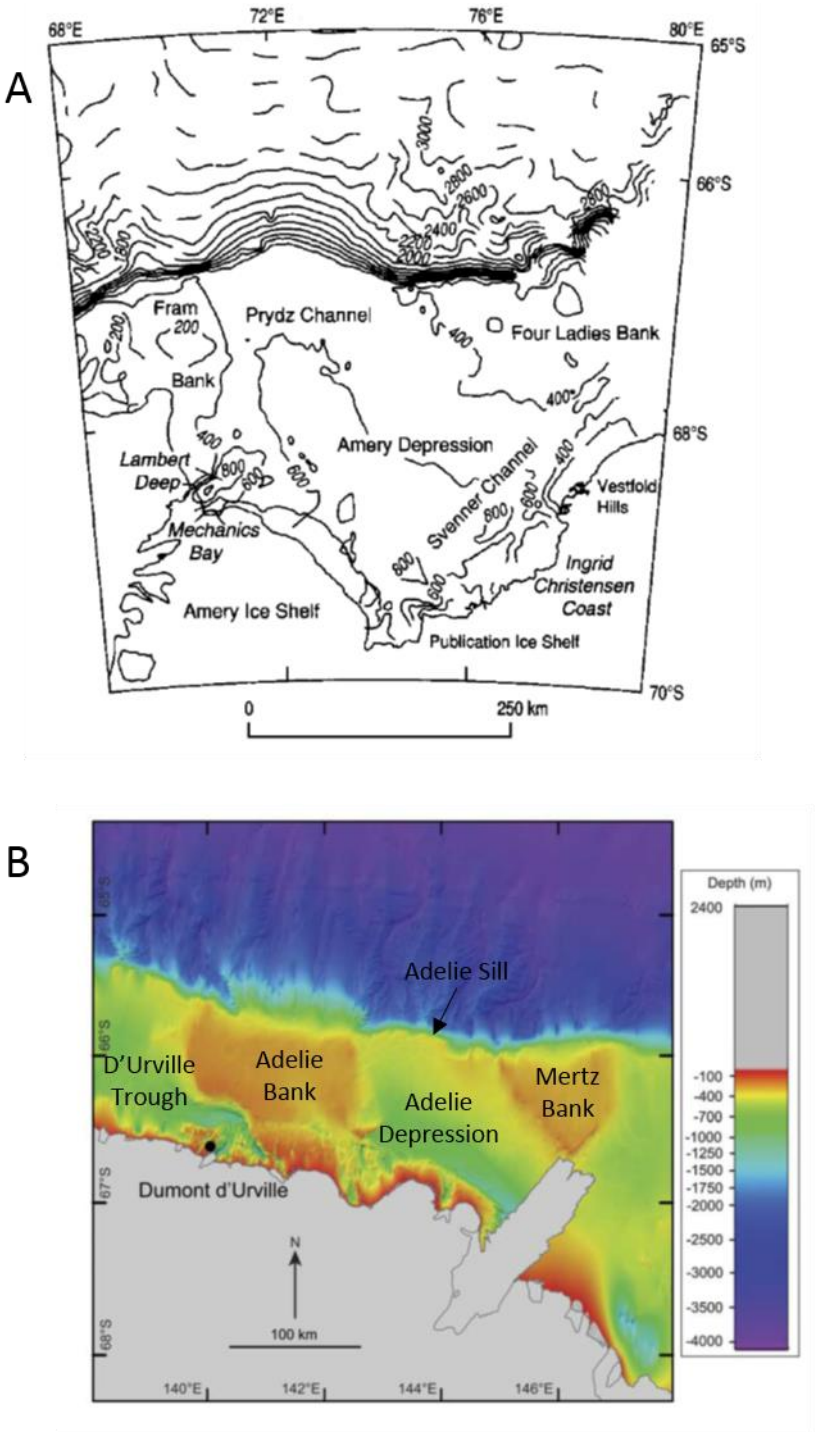


Figure 1.2. Bathymetric features of the (A) Davis site from O'brien and Leitchenkov (1997) and (B) the Dumont d'Urville site from Beaman et al. (2011).

2. Circulation and water masses

The Southern Ocean is one of the main drivers of the global thermohaline circulation (THC), which contributes to the world meridional redistribution of heat (Orsi *et al.* 1999; Marshall *et al.* 2008). The Southern Ocean therefore plays a fundamental role in the regulation of the global climate (Orsi *et al.* 1999; Marshall *et al.* 2008). This is dependent on a complex zonal and meridional hydrological circulation dominated by the Antarctic circumpolar current (ACC); the major feature in the Southern Ocean (Orsi *et al.* 1995, 1999; Marshall *et al.* 2008)(Fig. 1.3). The ACC flows clockwise (from west to east) far offshore (between 40°S and 65°S) around Antarctica (Orsi *et al.* 1995). It is itself sub-divided in three major fronts: the sub-Antarctic front (which sets the northern boundary of the Southern Ocean according to Deacon 1933), the Polar front and the southern boundary of the ACC (SB-ACC) (Orsi *et al.* 1995) (Fig. 1.3). In contrast, the inshore cold Antarctic coastal current circulates from east to west between the coast and the SB-ACC (Orsi *et al.* 1995; Nicol *et al.* 2006). The currents and water masses are separated by a series of frontal zones and the Antarctic coastal current is composed of a series of complex interlinked gyres rather than being a coherent zonal current (Orsi *et al.* 1995; Nicol *et al.* 2006). Moreover, the position and complexity of these hydrological boundaries are often defined by regional topographic and bathymetric features. This results in considerable meridional variations in hydrological regimes around Antarctica (Nicol *et al.* 2006).

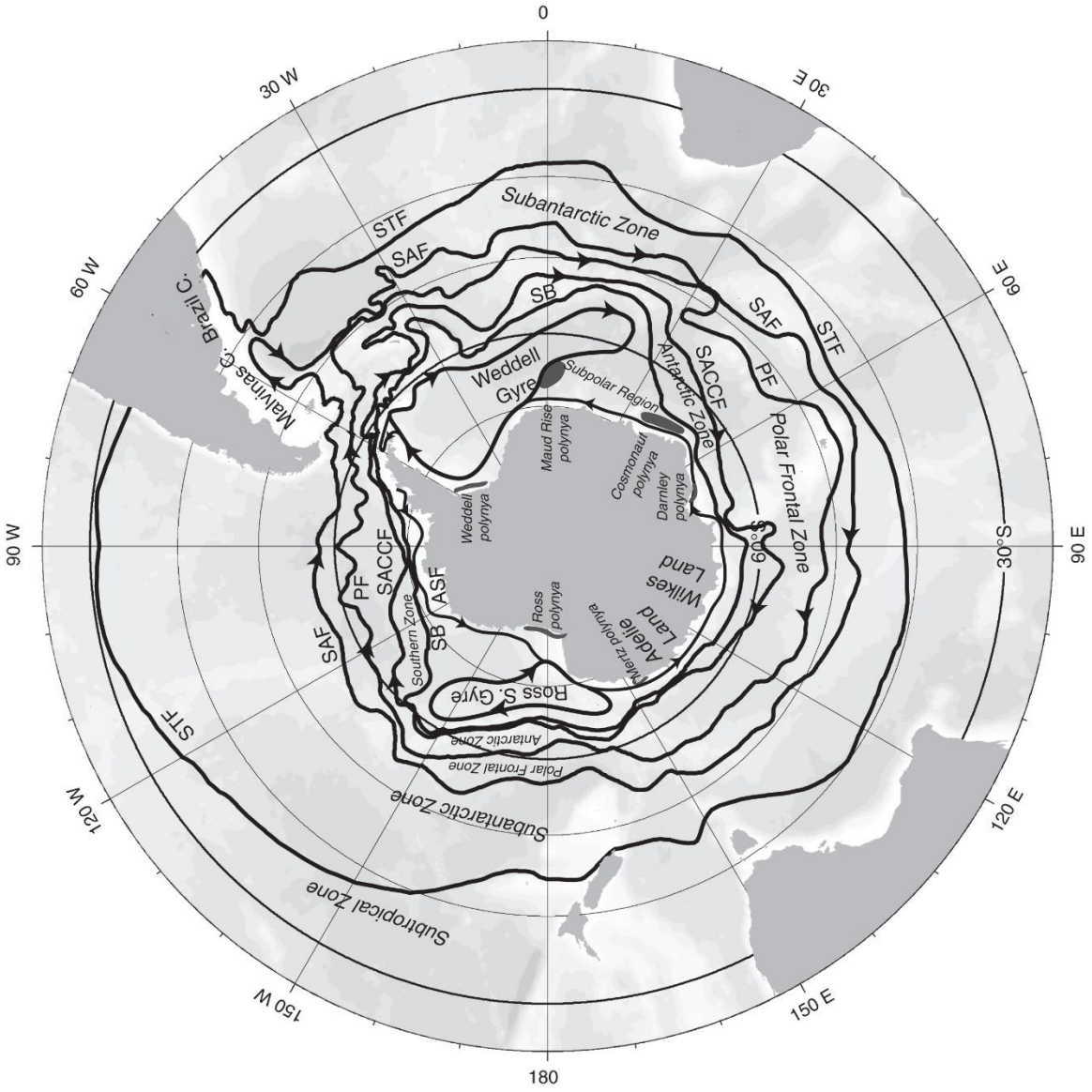


Figure 1.3. Southern Ocean geography and principal fronts from Talley et al. 2011 (Descriptive physical oceanography: an introduction, chapter 13). The Subtropical Front (STF) is the oceanographic northern boundary for the region. The eastward Antarctic Circumpolar Current (ACC) includes several fronts: Subantarctic Front (SAF), Polar Front (PF), Southern ACC Front (SACCF), Southern Boundary (SB). Front locations are taken from Orsi et al. (1995). The westward Antarctic Slope Front (ASF) (thin) follows the continental slope.

For instance, because there is little geographic variability along the coastline of the East-Antarctic region it is dominated by circumpolar circulation, unlike the Weddell and Ross seas, which are both characterized by a large embayment, and therefore influenced by large gyres (Nicol *et al.* 2006) (Fig. 1.3). This hydrological circulation appears to drive annual regional sea-ice extent, the position of oceanic boundaries, and biological productivity, resulting in the structuration of the pelagic Antarctic ecosystem (Nicol *et al.* 2000). Indeed, a winter survey conducted in East Antarctica revealed a positive relationship between the offshore distance of the SB-ACC and the maximal extent of winter sea ice (Nicol *et al.* 2000). Moreover, they found productivity at all levels (*e.g.* primary productivity, zooplankton, whales and seabirds) is also influenced and delimited by the SB-ACC. For instance, productivity occurs in a wider band where SB-ACC is located further offshore (*i.e.* western section of survey area [80-115°E] close to Davis), whereas productivity is concentrated nearer to the coast as the SB-ACC approaches the coast (115-150°E encompassing DDU) (Nicol *et al.* 2000).

The ACC also plays a crucial role in the formation of Antarctic Bottom Water (AABW). The AABW is the cold, dense and oxygen rich water mass laying in the abyssal layer, accounting for 30-40 % of the global ocean mass (Johnson 2008). AABW production is a key process of the THC, responsible for the ventilation and supply of nutrients to abyssal layers of the world's major oceans (Orsi *et al.* 1999; Williams & Bindoff 2003; Marshall *et al.* 2008; Ohshima *et al.* 2013) (Fig. 1.4). First, the warm and deep saline waters that originated in the northern hemisphere upwells at the south of each of the three global ocean basins and are transported around Antarctica by the ACC (Schmitz 1995) (Fig. 1.4). While surfacing, these circumpolar deep waters (CDW) mix along their path with the colder Antarctic surface water (ASW) thereby forming denser intermediate waters, known as modified circumpolar deep waters (MCDW) (Williams *et al.* 2008, 2010) (Fig. 1.5). Then,

AABW formation involves the formation of high salinity shelf waters (HSSW) from the pole-ward intrusions of MCDW trough deep bathymetric canyons and depressions over the continental Antarctic shelf (Williams *et al.* 2008, 2010) (Fig. 1.5). Brine rejection from sea-ice formation during winter is the major process of HSSW formation (Williams *et al.* 2008, 2010) (Fig. 1.5). Also involved, is the mixing with cold, fresh ice shelf waters (ISW) from ocean/ice interactions beneath ice shelves which increase the density of the HSSW enough that they sink (Williams *et al.* 2008, 2010) (Fig. 1.5). The newly formed AABW sinks to the abyssal layers, crosses the continental shelf break at specific locations and mix down the continental slope flowing equator-wards in each of the ocean sectors (Williams *et al.* 2008, 2010) (Fig. 1.4 and 1.5). The conversion of MCDW into the cold, saline AABW only occurs in several unique locations around Antarctica (Fig. 1.4). These include the Weddell sea (71%) (Foster & Carmack 1976; Fahrbach *et al.* 1995; Foldvik *et al.* 2004), the Ross sea (6%) (Jacobs *et al.* 1970; Whitworth & Orsi 2006), as well as two locations that encompass the two focal study sites within East Antarctica: the Adelie Land coastline (23%) (where DDU is located; (Williams *et al.* 2008, 2010) and the Prydz bay (where Davis is located) which could account for 6-13 % of AABW production (Ohshima *et al.* 2013). Thus, East Antarctica is a major contributor to AABW formation.

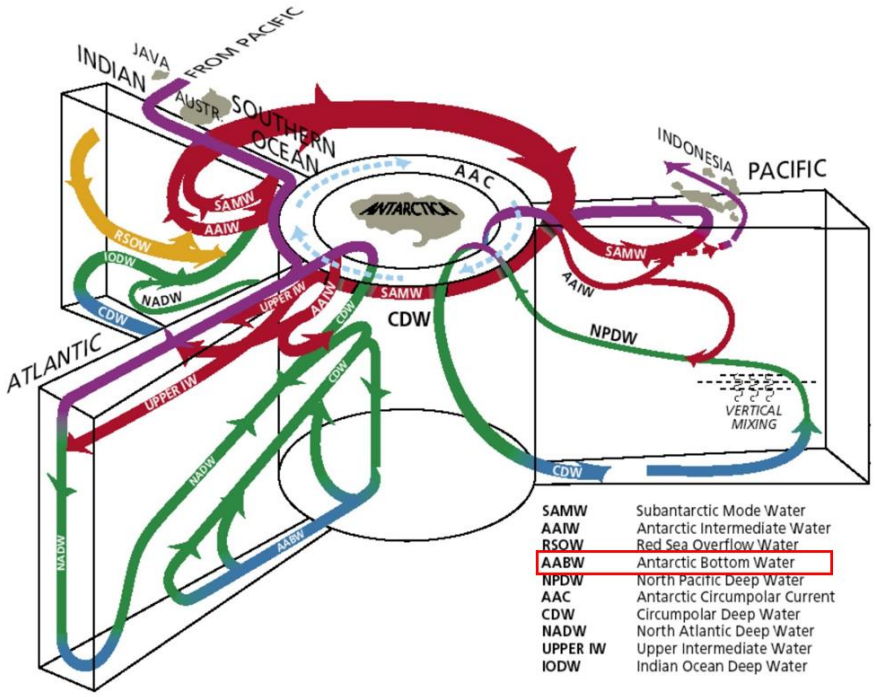


Figure 1.4. The global thermohaline circulation around Antarctica from Schmitz (1995), highlighting in particular the circulation of Antarctic Bottom Water.

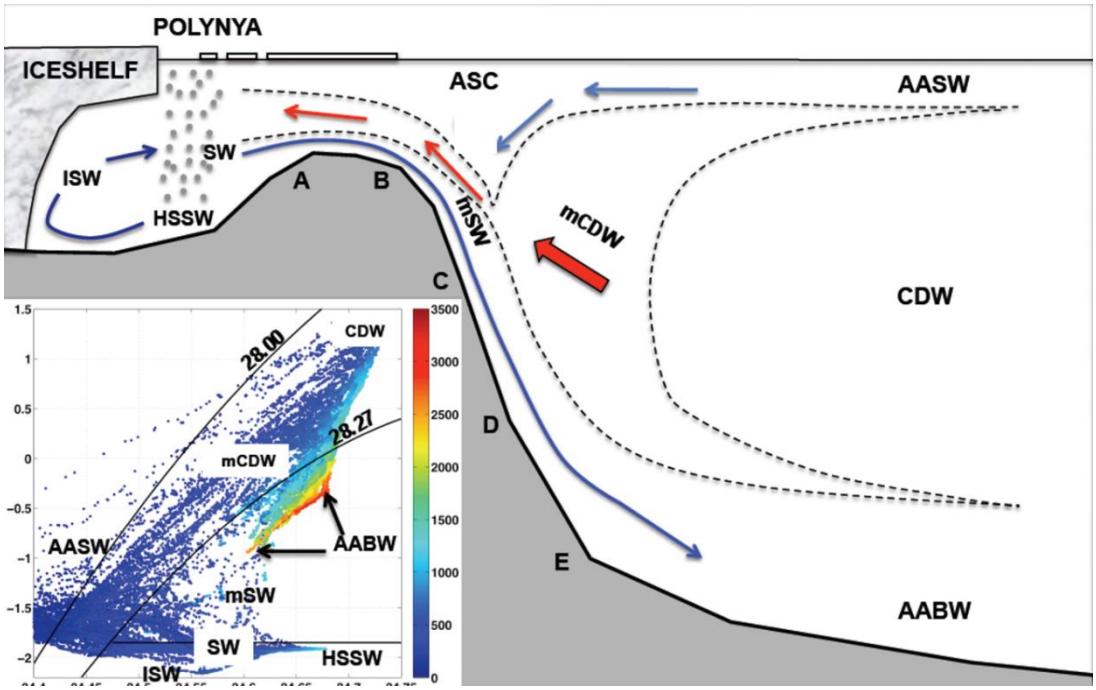


Figure1.5. Antarctic bottom water formation on the Antarctic continental shelf from Williams et al. (2010).

In some locations such as the Prydz bay and Adelie land, the formation of dense water is tightly linked to large coastal polynya systems (*i.e.* areas of open water within the sea-ice; Mertz Glacier polynya in Adélie Land and Cape Darnley polynya in Prydz bay) that results in intense ice production, and therefore, enhanced brine release into the water column (Fig. 1.6) (Williams *et al.* 2008, 2010; Ohshima *et al.* 2013). Another dominant factor is the onshore flow of MCDW on the shelf, allowed by the regional bathymetric features (*i.e.* presence of deep canyons and depressions), which increases shelf water salinity, and potentially supplies sufficient heat to help maintain the polynya (Rintoul 1998 p. 199; Williams & Bindoff 2003) (Fig. 1.6). In combination, these processes greatly increase the salinity of the shelf water, enhancing HSSW production (Williams *et al.* 2008; Ohshima *et al.* 2013). Over time, the volume of dense shelf water increases and accumulates in bathymetric depressions (*i.e.* Adélie depression in Adelie Land) until it spills over the shelf break (*e.g.* the Adelie sill in Adelie Land) and descends to the abyssal layer (Fig 1.6) (Williams *et al.* 2008, 2010; Ohshima *et al.* 2013).

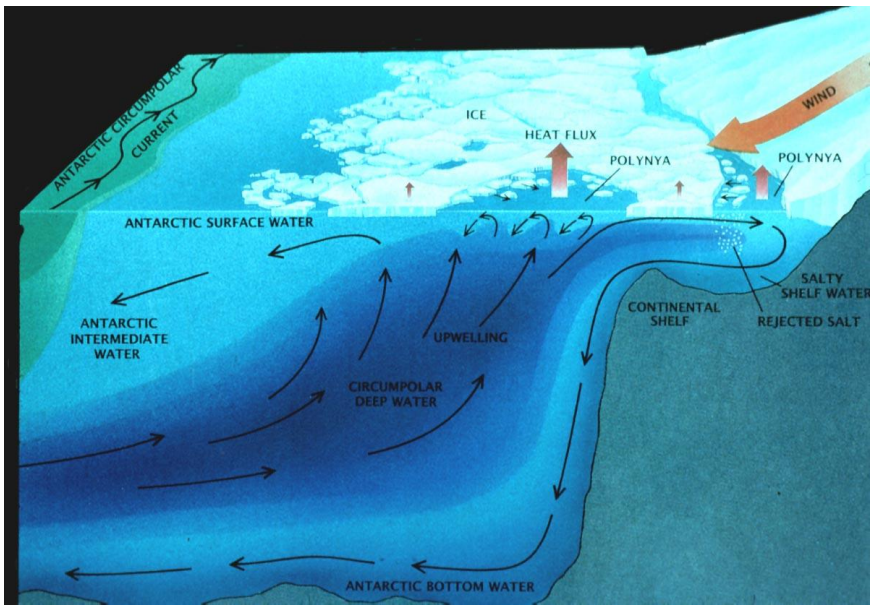


Figure 1.6. Antarctic Bottom Water formation beneath coastal polynya *(Comiso & Gordon 1998)*

3. Sea-ice environment

Sea-ice is a substrate, which after initial freezing of sea water, is profoundly modified by interactions between physical, biological and chemical processes (Dieckmann & Hellmer 2010). Antarctic sea-ice is highly dynamic that extends from hundreds to thousands of kilometres from the land in winter, before melting and receding back towards the shore in summer. Indeed, its annual expansion varies from ~ 19 million km^2 in September (end of winter) to only ~ 4 million km^2 remaining in February (end of summer) (Comiso & Nishio 2008) (Fig. 1.7). This represents one of the greatest seasonal changes in physical properties anywhere on Earth (Nicol *et al.* 2006; Massom & Stammerjohn 2010). However, in some locations, such as the Weddell and the Amundsen sea, the sea-ice persists over years (Fig. 1.7).

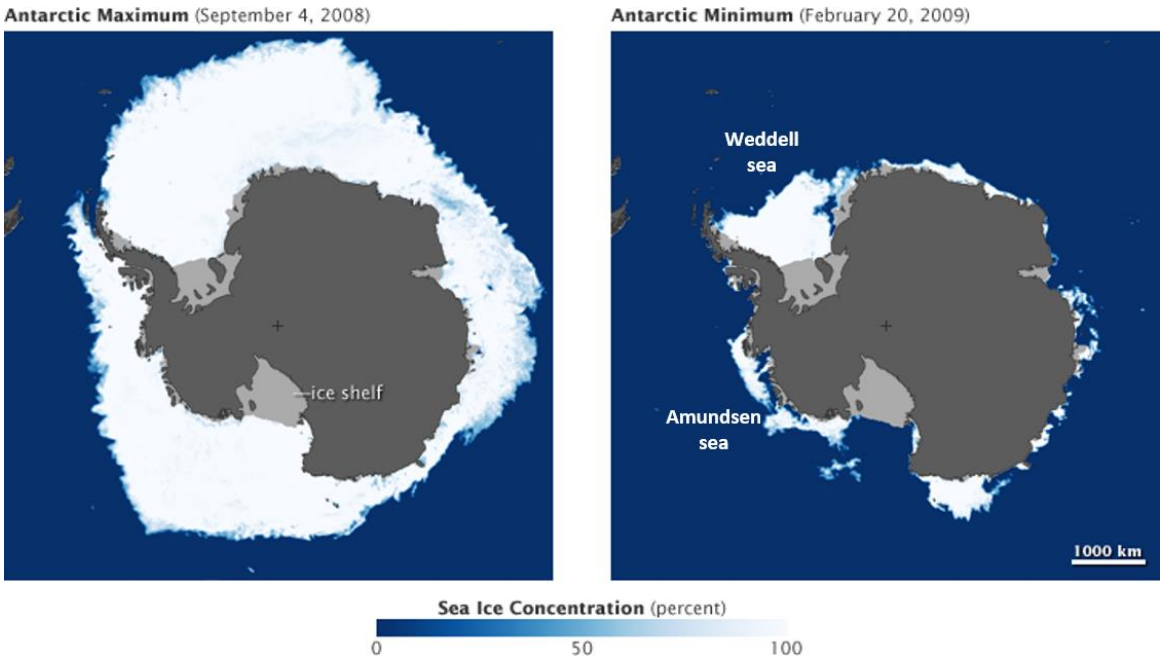


Figure 1.7. Seasonal changes in sea-ice extent from September to February (Comiso and Nishio 2008). Image taken from the NASA earth observatory website: www.earthobservatory.nasa.gov

Sea-ice and its snow cover form an insulate, high-albedo ‘blanket’ on the ocean surface, acting as a physical barrier that seasonally modulates (but is also controlled by) ocean-atmosphere momentum, exchanges of gases, as well as moisture and heat fluxes (Dieckmann & Hellmer 2010; Massom & Stammerjohn 2010; Arrigo 2014). Moreover, seasonal brine rejection from intense sea-ice formation is a key process in AABW production which is a crucial driver of the global ocean circulation (Rintoul 1998; Williams *et al.* 2008). Thus, through its extent, structure and seasonality, sea-ice plays a critical and highly dynamic role in the global climate system, as well as on the ecology of the Southern Ocean ecosystem (Massom & Stammerjohn 2010). However, because it is relatively thin, sea-ice is vulnerable to small perturbations within the ocean and/or atmosphere, which can significantly change its extent and thickness. Sea-ice has therefore become one of the most (if not *the* most) important component in climate research (Dieckmann & Hellmer 2010).

Sea-ice cover and characteristics vary both from the open-ocean to the continent and around Antarctica. Two major types of sea-ice can be distinguished: the pack-ice and the fast-ice. The pack-ice is the seasonal sea-ice that forms offshore and melts every year. Despite regional variability, pack-ice thickness is approximately 0.5-1 m (Nicol *et al.* 2006). The circumpolar Antarctic pack-ice zone is highly dynamic and is composed of assemblages of floes of differing sizes that constantly drift at typical rates of ~15-20 km per day (Heil & Allison 1999). In contrast, the fast-ice persists all year round, forms in the coastal area over a narrow zone (a few km to 200 km wide), and is attached to the land, iceshelf or grounded icebergs. The fast-ice and multi-year ice constitute a thicker (1-3 m) and relatively stationary platform compared to the pack-ice (Nicol *et al.* 2006; Massom & Stammerjohn 2010).

The winter Antarctic sea-ice environment is also characterized by the presence of polynyas. Adjacent to the coast, these are called ‘latent heat’ polynya because they are

predominantly formed and maintained by strong katabatic winds. These severe ocean-ward winds can reach speeds of up to 80 knots and continuously advect the newly formed sea-ice away from the coastal winds (Nicol *et al.* 2006; Tynan *et al.* 2009; Massom & Stammerjohn 2010) (Fig. 1.8). Upwelling of relatively warm water from below can also provide heat fluxes that contribute to the maintenance of these coastal polynyas. This may occur, for example, in regions where intrusions of the warmer MCDW flow onto the shelf. As well as polynyas close to the coast, some may also occur offshore if they are purely driven by sensible heat fluxes. These 'sensible heat' polynyas occur in regions where there is sufficient oceanic heat at the surface to prevent sea-ice forming (Nicol *et al.* 2006; Tynan *et al.* 2009; Massom & Stammerjohn 2010) (Fig. 1.8). Typically this occurs in regions of upwelling, vigorous vertical mixing, or where there is a strong interaction between ocean currents and topographical features. Polynias are important regions for several reasons; first they represent regions of high sea-ice production and, in certain locations, are associated with AABW production; second they represent ventilation windows between the deep ocean and atmosphere; and finally they are important regions for biological activity (Nicol *et al.* 2006; Tynan *et al.* 2009; Massom & Stammerjohn 2010).

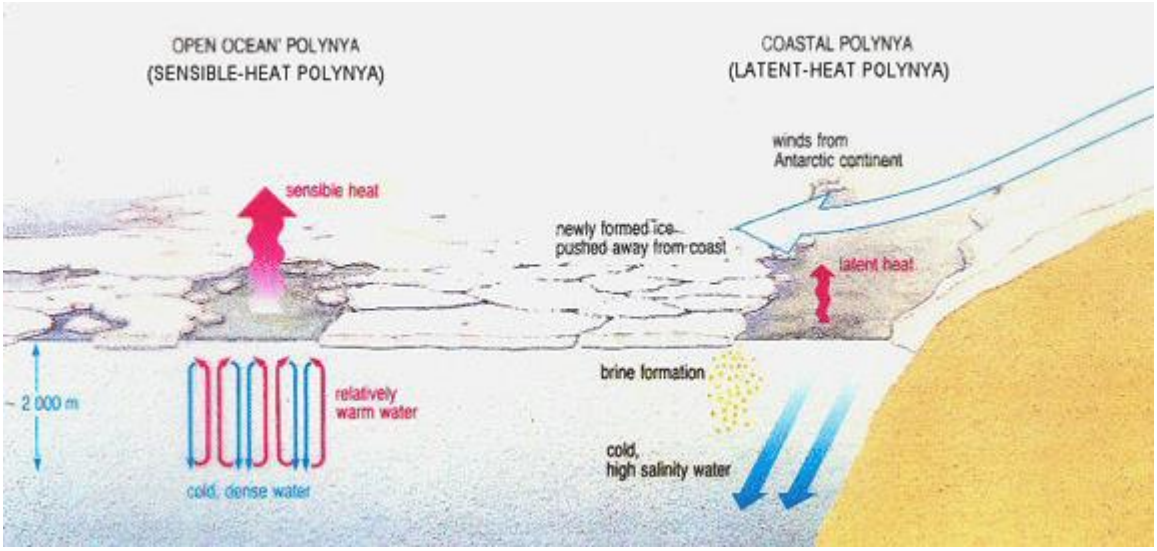


Figure 1.8. Diagram of sensible-heat (open-ocean) and latent-heat (coastal) polynya formation. Image from *Ocean Circulation, 2nd Edition* by Open University, Butterworth-Heinemann Publishers, page 219.

B - Sea-ice dependent pelagic ecosystem

1. Sea-ice community

Sea-ice plays a pivotal role in the biogeochemical cycles of the Southern Ocean and in the structure and dynamics of Antarctic marine ecosystems (Massom & Stammerjohn 2010). Depending on whether the conditions under which sea-ice forms are calm or turbulent will determine sea-ice crystal structural variety and composition (Arrigo 2014). Indeed, the same processes that trap sea-water within the sea-ice matrix during its initial formation also trap dissolved nutrients such as nitrate, phosphate, silicate and trace metal such as iron (iron is particularly important for proliferation of primary producers). These nutrients can also be brought to the porous ice structure after it formed by tidal currents and other advective processes (Cota & Horne 1989). For instance, due to its annual extend-retreat cycle, the pack ice interacts with several physical features (*e.g.* the ACC, the Antarctic divergence, the continental shelf-break or the Antarctic coastal current) that induce water masses and nutrient upwelling, which can in turn be trapped in the sea-ice (Massom & Stammerjohn 2010). Finally, dust deposited on the surface of the ice contains relatively small amounts of macronutrients, as well as relatively large amounts of trace metals such as iron (Arrigo 2014).

These nutrients may be used directly by the within-ice community or made available to the pelagic ecosystem in spring when sea-ice melts (Arrigo 2014). In addition to releasing nutrients in the water-column, sea-ice enhances primary production and generates extensive phytoplankton blooms in spring as it melts by inducing stratification of surface waters, thereby retaining the phytoplankton within the well-lit surface layer (Nicol *et al.* 2006; Massom & Stammerjohn 2010; Arrigo 2014). Sea-ice itself is colonized

by several species of autotrophs, bacteria, heterotrophic protists as well as metazoans such as copepods that are also released in the water column in spring (Bluhm *et al.* 2010; Arrigo 2014). But more importantly for the pelagic ecosystem during winter, the bottom of the sea-ice is colonized by sea-ice algae. Indeed, sea-ice algae biomass can be very large; up to three times more abundant than in the water column (Smith *et al.* 2007; Quetin & Ross 2009). In addition, exopolysaccharides contained within sea-ice, which are produced (and used) by the sea-ice community, can be used by diatoms to grow in both the light and dark; a crucial advantage under conditions of light limitation or during overwinter survival (Palmisano & Garrison 1993; Meiners *et al.* 2003). These bottom sea-ice algae therefore provide a crucial source of food for grazers when other resources are low in the water column. Thus, the ice–water interface is a favoured habitat for diverse crustaceans such as copepods, amphipods and euphausids (*e.g.* Antarctic krill, *Euphausia superba*), as well as small fishes (Bluhm *et al.* 2010; Arrigo 2014). In turn, these species represent a source of food for top predators or/and the prey they rely on (Tynan *et al.* 2009).

2. Upper trophic levels depending on sea-ice habitat

Zooplankton, particularly those greater than 0.2 mm in length, provide the main trophic link between the primary producers and apex predators in the Southern Ocean (Ducklow *et al.* 2007).

2.1 The Antarctic continental shelf assemblages

On the shelf, this link is mainly made by ice krill (also known as "crystal" krill, *Euphausia crystallorophias*); the most important grazer of neritic diatoms (Pakhomov & Perissinotto 1997) and potentially ice algae (not well documented) (Smith *et al.* 2007). Ice krill can also supplement its dietary requirement during winter by utilizing decaying material from zooplankton (Vallet *et al.* 2011). Ice krill is the main component of silver fish diet (Hubold 1985) but can also be consumed directly by some predators (e.g. Adélie penguins *Pygoscelis adeliae*, crabeater seals *Lobodon carcinophaga* and minke whales *Balaneoptera bonaerensis*). The Antarctic silverfish occupies a critical role in the Antarctic food web, as sub-adults represent more than 90% of the biomass of mid-water fish (DeWitt 1970). It is consumed by flighted birds (South polar skuas *Stercoriarius maccormicki*, snow petrels *Pagrodoma nivea* and Antarctic petrels *Thallassoica antarctica*), Adélie and emperor (*Aptenodytes forsteri*) penguins, Weddell seals (*Leptonychotes weddellii*), Antarctic toothfish (*Dissostichus mawsoni*) and other fishes, as well as minke and killer whales (*Orcinus orca*) (Smith *et al.* 2007). In the absence (or low availability) of ice krill in space and time, the Antarctic silverfish may instead dominate energy transfer within the water column (Smith *et al.* 2007). Another notothenioid commonly found on the shelf is the large Antarctic toothfish (~ 2 m long and >100 kg as adults), which feeds on Antarctic silverfish as well as cephalopods and mysids (Smith *et al.* 2007, 2014). It is epibenthic but also occurs in mid-water depths under the fast-ice (Fuiman *et al.* 2002). In the Ross sea, it is a major food item for Weddell seals and killer whales (Pitman & Ensor 2003; Ainley & Siniff 2009a). The cryopelagic notothenioid, *Pagothenia borchgrevinki*, inhabits the underside of sea-ice where they use ice crevasses to escape from their predators (e.g. Weddell seals, skuas and emperor penguins) (Smith *et al.* 2007). Several species of top predators can be found on the Antarctic shelf. The ice-obligate emperor and Adélie

penguins, and “pack-ice” seal species (Ross, crabeater, leopard and Weddell seals) rely on the sea-ice to rest, feed and breed, and therefore are associated with sea-ice year-round (Tynan *et al.* 2009). However, emperor penguins and Weddell seals are the only inhabitants of the fast-ice during winter (Burns & Kooyman 2001). During winter, other top predators such as minke and killer whales, as well as flying sea-birds cited previously, leave the Antarctic shelf owing to darkness and thick ice (Smith *et al.* 2007; Tynan *et al.* 2009).

2.2. The Antarctic shelf-break assemblages

The shelf break represents a marked change between oceanic and neritic pelagic assemblages. We saw that the Antarctic continental shelf assemblages was dominated by ice krill, notothenioids fish (mainly the Antarctic silverfish *Pleurogramma antarcticum*). In contrast, the oceanic assemblages are dominated by meso- and bathypelagic fish, mainly myctophids (Koubbi *et al.* 2011; Moteki *et al.* 2011). Finally, the shelf break is composed of a mixture between oceanic and neritic assemblages where notothenioid and myctophids fish can interact when foraging on large swarms of Antarctic krill (*Euphausia superba*) (Koubbi *et al.* 2011; Moteki *et al.* 2011). Sea-ice is a major determinant of Antarctic krill distribution as its life cycle is tightly linked to the seasonality of sea-ice (Quetin & Ross 2009). For instance, during winter, larval and juvenile krill, that cannot withstand the prolonged fasting period sustained by adults, are found on the underside of sea-ice where they feed on ice algae and animals of the sea-ice microbial community (Quetin & Ross 2009). Consequently, the circumpolar distribution of krill is generally bounded by the maximum extent of pack-ice (Quetin & Ross 2009), which in some regions (*e.g.* East-Antarctica) is in turn influenced by the position of the ACC fronts such as the SB-ACC (Nicol *et al.* 2000; Nicol & Raymond 2012). In contrast to the coastal neritic zone, over the

shelf slope Antarctic krill becomes the dominant species of meso-zooplankton and is a keystone species of the ecosystem associated to the pack-ice zone where Adélie penguins, minke whales and crabeater seals congregate during winter (Chapman *et al.* 2004; Everson 2008; Ribic *et al.* 2008). Antarctic krill is also consumed by flying sea-birds such as albatrosses and seabirds (Croxall 1987). All Antarctic seals depend somewhat on krill either by consuming it directly or indirectly via their prey such as fish and squid (Everson 2008). For instance, the mesopelagic myctophid *Electrona antarctica*, particularly abundant on the shelf break area, is an important predator of krill and is in turn preyed upon by top predators (*e.g.* SES) (Barrera-Oro 2002; Moteki *et al.* 2011; Constable *et al.* 2014). The squid, *Psychrotheutis glacialis*, can also be important to predators near the shelf break (*e.g.* SES and sperm whales *Physeter macrocephalus*) (Tynan 1998; Tynan *et al.* 2009; Constable *et al.* 2014). Some other species such as the southern elephant seals (SES *Mirounga leonine*) and the Antarctic fur seal can forage over winter in marginal ice zones (*i.e.* areas covered by ice close to open water), on the shelf break, or on the continental shelf in the case of some SES males (Boyd *et al.* 1998; Bailleul *et al.* 2007). However, these animals will ultimately return to land for the breeding season.

C - Studying the foraging ecology of top predators

1. Foraging in a heterogeneous environment

In the simplest form, the habitat of an organism is the place where it lives (Odum *et al.* 1971). More specifically, a habitat is the sum of the specific resources and conditions that result in occupancy and that are needed by an organism for its successful reproduction and survival (Krausman 1999). Habitat use can be defined as the way an animal uses a collection of environmental components to meet its life requisites. **An animal can exhibit several activities within its habitat (*e.g.* resting, breeding, escaping, feeding), however, foraging activity is one of the most important because obtaining adequate food supply is a basic requirement of all other life-history traits** (Stevick *et al.* 2002). Therefore, each species adopts foraging strategies and selects environmental features associated with the resources needed to maximise its reproductive success and survival (Krausman 1999). Thus, habitat selection is an active behavioural process that results from a compilation of innate and learned behaviours (Wecker 1964).

Environmental features of a habitat vary at different spatial and temporal scales that directly influence the distribution, abundance, and therefore, availability of resources (*e.g.* Bost *et al.* 2009). Thus, in the environment, resources are heterogeneously distributed and aggregated in "patches" of differing sizes and associated with varying densities of prey. Moreover, these patches are organized following a hierarchical and nested structure of smaller patches contained within larger patches. These patches vary both in space and time at scales that depend on the physical parameters that structure them (Fauchald *et al.* 2000; Fauchald & Tveraa 2006). For instance, in the marine environment, the spatial distribution of schooling fish and krill is typically organized in such a nested patch hierarchies (Murphy

et al. 1988; Fauchald & Erikstad 2002). At the smallest scale, individuals are aggregated into schools and swarms (Fig. 1.9). These schools and swarms are themselves aggregated into patches resulting from meso-scale oceanographic features (*e.g.* fronts, eddies) (Fig. 1.9). Finally, these patches are contained within large-scale areas that reflect a particular habitat boundary (Fauchald & Tveraa 2006) (Fig. 1.9). **Therefore, at small scales one would expect predators to adjust their behaviour according to the perception of prey, whereas at larger scales they are likely to rely on physical and/or biological cues (*i.e.* increased productivity, presence of prey, quality of prey patch) of the environment that are associated with better prey predictability** (Fauchald & Tveraa 2006; Bost *et al.* 2009)**.**

In an environment where prey are patchily distributed, such as the open ocean, predators must continuously adjust their foraging behaviour according to the distribution and availability of their prey in order to maximize resource acquisition (Charnov 1976; Fauchald *et al.* 2000; Fauchald & Erikstad 2002). Moreover, a predator's costs associated with travelling from one patch of prey to another and pursuing a prey must be compensated with food intake (MacArthur & Pianka 1966).

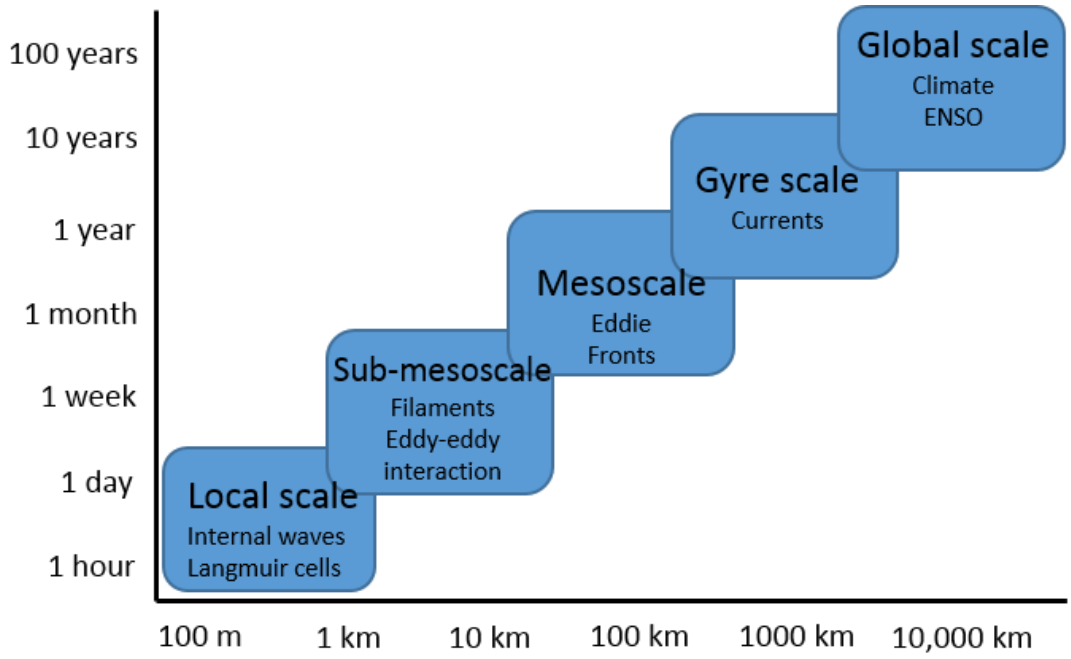


Figure 1.9. Spatial and temporal scale of main oceanographic processes (see Cotté 2009 [PhD])

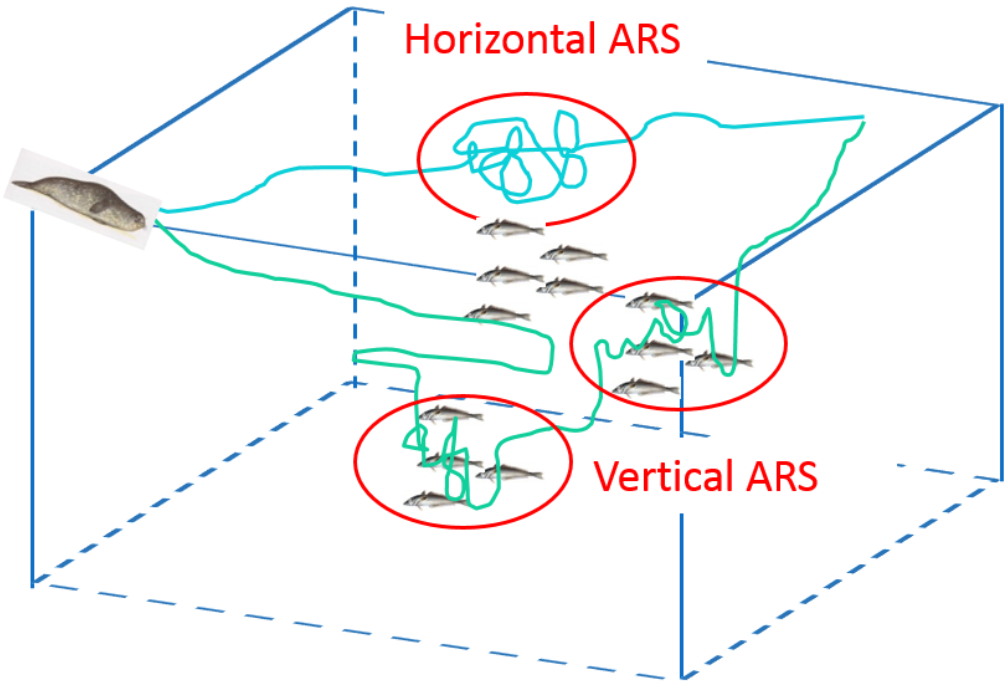


Figure 1.10. Schematic of Area restricted Search behaviour in the horizontal and vertical dimensions.

Thus, one aspect of optimal foraging strategy suggests predators will maximize the time spent in the vicinity of a successful prey patch by decreasing their displacement speed and increasing their turning frequency (Kareiva & Odell 1987; Fauchald & Tveraa 2003) (Fig. 1.10). This behaviour, called "area restricted search" (ARS), is frequently observed in free ranging animals in the horizontal dimension (Fig. 1.10). However, in the marine environment, resources are heterogeneous both in the horizontal and vertical dimensions. Therefore, we expect marine predators to adopt ARS behaviour not only along their track, but also while diving (Fig. 1.10).

2. Detection of foraging behaviour

Foraging is of central importance in ecology because it determines energy gains, and ultimately, the fitness of an animal. Understanding where, how and when top predators forage is also fundamental to identify favourable habitats and assess how environmental changes (*i.e* climatic and anthropogenic) would affect individuals and population dynamics. However, detecting foraging activity is a challenging task in the marine environment because marine predators spend most of their time at sea, and feed on prey aggregated at depth. Studying the foraging behaviour of polar species present additional challenges with respect to logistics and difficulty to see them in sea-ice covered areas.

In the last decades (since the late 1960's, Kooyman 1965) the development and improvement of new technologies have allowed researchers to follow the movements of marine predators over great distances and long periods of time at increasing resolutions (Evans *et al.* 2012; Costa *et al.* 2012). In combination with the concurrent development of

statistical and analytical analyses, data collected from archival and satellite tags have greatly increased our knowledge on the at-sea ecology of marine predators (Evans *et al.* 2012; Costa *et al.* 2012).

2.1 Inferring foraging activity from tracking data

Tracking information of animals at sea are provided by a broad range of telemetric tools such as the Global Positioning System (GPS), Argos satellite system, light-based geo-location or acoustic tracking (Costa *et al.* 2012). These data can be used to determine the different habitats used by an animal along its trajectory and identify foraging grounds. Residence time (estimated as time spent per unit area), first passage time and fractal analyses, as well as process based models (*e.g.* State-space, Hidden Markov and Lévy flights models), are commonly used to infer foraging activity from tracking data (Viswanathan *et al.* 1999; Fauchald & Tveraa 2003; Jonsen *et al.* 2005; Tremblay *et al.* 2007; Johnson *et al.* 2008). These approaches rely on the assumption that an individual will increase its time spent searching for food in more profitable prey patches and therefore identify ARS behaviours (*i.e.* reduced speed and increased track sinuosity) along an individual's track. **However, depending on the species and environmental conditions, inferring foraging success from horizontal tracking data only (*i.e.* surface locations) is not always possible, and could be misleading in identifying the true foraging activity that occurs at depth** (Robinson *et al.* 2007; Weimerskirch *et al.* 2007; Bastille-Rousseau *et al.* 2010)**. This is particularly true in places where environmental conditions could constrain animal movements such as ice-covered areas** (Bailleul *et al.* 2008)**.** In the case of a seal diving under heavy ice, sinuous and slow movements observed at the surface could lead to the identification of false ARS.

2.2 Direct measurements of foraging success

The fine-scale foraging success of marine predators has been investigated using oesophageal and stomach temperature sensors (Wilson *et al.* 1995; Charrassin *et al.* 2001; Horsburgh *et al.* 2008), Hall sensors (*i.e.* jaw magnets) or accelerometers to detect mouth opening events (Wilson *et al.* 2002; Viviant *et al.* 2009; Naito *et al.* 2010), as well as more direct evidence such as video cameras (Marshall 1998; Davis *et al.* 1999). These direct observations of interactions with prey and/or feeding events provide new insights into the vertical foraging behaviour of marine predators. However, these loggers can be difficult to deploy, are expansive and can be considered as intrusive (*e.g.* because of their size such as the crittercam or because they imply surgery procedures). In addition, these loggers need to be retrieved, which is often not practical. For these reasons, these loggers have generally been deployed on a limited number of individuals and for short durations (until recently, see Naito *et al.* 2013). Swim speed and acceleration data allow through dead-reckoning analysis to reconstruct the underwater 3D movements of diving predators (Mitani *et al.* 2003; Wilson *et al.* 2007). This data can also be used to quantify the energetics expenses associated with the dive (Wilson *et al.* 2007). Recently, head mounted accelerometers have proven to be efficient in detecting prey capture attempts in pinnipeds and penguins (Viviant *et al.* 2009; Watanabe & Takahashi 2013a) and have been used to study the fine scale foraging behaviour of top predators over long durations (Guinet *et al.* 2014). However, until these types of data become more widely available most studies will still rely on time-depth information to infer predator foraging behaviour at depth.

2.3 Inferring foraging activity from diving behaviour

Dive profiles recorded from archival data loggers or satellite relayed time-depth recorders have been widely acquired and still provide valuable information on foraging activity inferred from dive metrics (*see* Figure 1.11) (Dragon et al., 2012; Hindell et al., 1991; Le Boeuf et al., 1988; Scheffer et al., 2012; Schreer et al., 2001) or a combination of those (*e.g.* residuals of bottom time, see Bailleul *et al.* 2008). Based on these metrics and dive shapes, several studies have assigned a dive to one of three behaviours: foraging, transiting, and resting (Le Boeuf *et al.* 1988; Hindell *et al.* 1991; Schreer *et al.* 2001). Most of these methods and indices rely on the assumption that marine predators optimize their foraging activity at depth by increasing the time spent at the maximum depth of their dive while minimizing the time spent in transit (*e.g.* descent/ascent phases of a dive) (Houston & Carbone 1992; Thompson *et al.* 1993; Schreer *et al.* 2001; Watanabe *et al.* 2003).

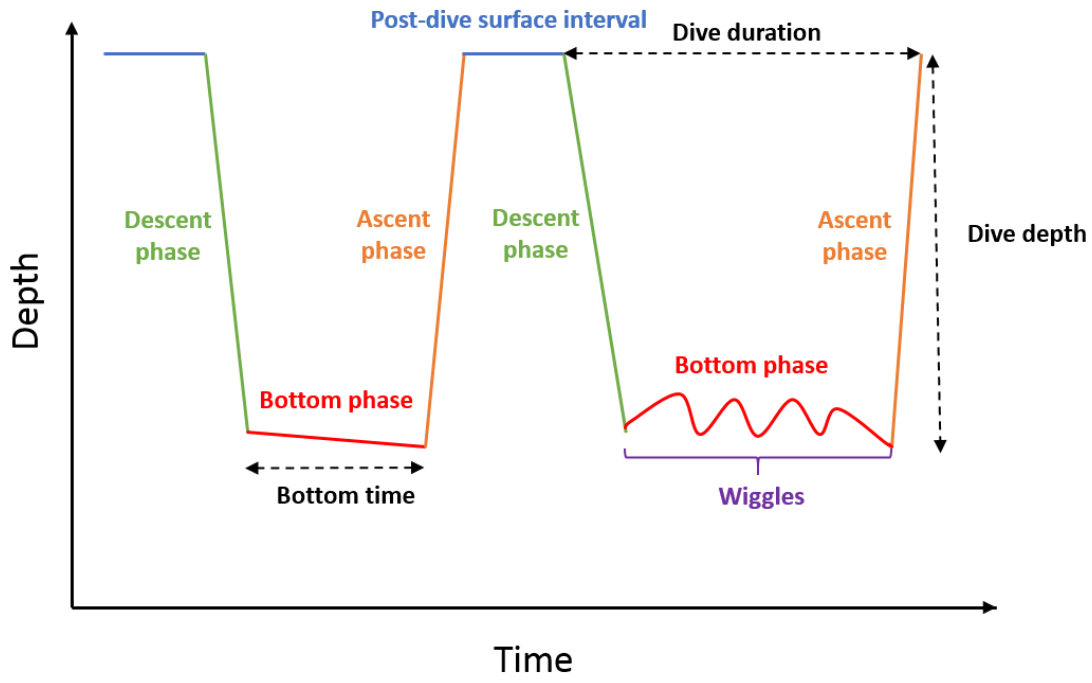


Figure 1.11. Schematics of dive profiles and the dive metrics that can be calculated from it.

The bottom phase of dives has been independently validated as the time when most feeding occurs in several species (*e.g.* Antarctic fur seals (*Arctocephallus gazella*) (Hooker *et al.* 2002), northern elephant seals (*Mirounga angustirostrisi*) (Kuhn *et al.* 2009), grey seals (*Halichoerus grypus*) (Austin *et al.* 2006), Weddell seals (Watanabe *et al.* 2003)). Other studies showed that feeding events for different penguins, whales and pinnipeds are associated with "wiggles" (Simeone & Wilson 2003; Goldbogen *et al.* 2006; Bost *et al.* 2007; Calambokidis *et al.* 2007; Hanuise *et al.* 2010; Watanabe & Takahashi 2013a). When a marine predator is spending some time at a particular depth and increasing the vertical sinuosity of its path while at this depth ("wiggles"), it corresponds to vertical ARS behaviour (*i.e.* Fig. 1.10). **Similar to the horizontal ARS concept, changes in vertical movement patterns may also be useful to detect foraging activity along the whole dive profile, rather than only considering pre-determined "foraging" parts of it (*e.g.* bottom phase).**

3. Habitat use of top predators

The Southern Ocean offers a wide range of habitats that vary from open water to ice covered areas; oceanic and neritic domains associated with complex bathymetry and different ecosystem assemblages; as well as multiple hydrological features (*e.g.* water masses, fronts, eddies, ACC) (see sections "Winter Antarctic environment" and "Sea-ice dependant pelagic ecosystem"). These environmental features are highly dynamic and exhibit seasonal variations. They also structure the spatial and temporal distribution of resources at different scales according to the environmental parameter considered (see section "Optimal foraging in a heterogeneous environment" and Fig. 1.9).

Marine mammals and seabirds are some of the best studied taxa in the Southern Ocean (Trathan *et al.* 2007; Constable *et al.* 2014). There are several reasons for this intensive effort. First, studying top predator ecology is crucial to understand how they adapted to their environment, particularly in polar regions where the environment (darkness, cold, sea-ice covered areas, strong winds) is so challenging. Second, the functioning of marine ecosystems depends on bio-physical couplings which ultimately affect the performance and population dynamics of top predators. Moreover, top predators are long-lived species dependent upon an extensive set of trophic links within the wider trophic web. Therefore, they are assumed to integrate the spatio-temporal variations of the underlying trophic levels. This would be reflected by top predators' foraging behaviour and ultimately individual and population dynamics. These attributes make them valuable sentinels of an ecosystem's status and change (Hindell *et al.* 2003; Trathan *et al.* 2007; Durant *et al.* 2009). **Studies on habitat selection and use are essential for understanding the biological requirements of animals and the strategies they use to fulfil their need. In addition, information on patterns of habitat use is crucial for conservation and management purposes. However, this requires our ability to (i) detect foraging activity (see section "detection of foraging" and (ii) relate foraging behaviour to the environmental features at an appropriate spatio-temporal scale** (Fauchald & Tveraa 2003, 2006).

Improvements in bio-logging technology (*e.g* miniaturization of devices, extended battery life, integration of new sensors) enable high quality *in situ* environmental data (*e.g.* temperature, conductivity, ambient light, fluorescence) and 3-dimensional movements of predators to be recorded simultaneously (Costa *et al.* 2012) (*e.g.* Fig. 1.12). **This is particularly useful for investigating marine top predator habitat use and how physical environmental features can influence their foraging behaviour** (Charrassin & Bost

2001; Fedak 2004; Bost *et al.* 2007; Biuw *et al.* 2010)**. In addition, these predators acquire valuable environmental data in remote and severely under-sampled regions, which are difficult to access otherwise (*e.g.* sea-ice covered areas)** (Charrassin *et al.* 2008; Ohshima *et al.* 2013; Roquet *et al.* 2013)

Figure 1.12. Weddell seal equipped with a CTD-SRDL tag (left) (Conductivity Depth Temperature – Satellite Relayed Data Logger) and details of the sensors on the tag (right)

Over the last ten years, large international tag deployment programs have already improved our understanding of links between foraging behaviour of top predators and key biotic and abiotic features of the environment (*e.g.* hydrology, topography and sea-ice) (*e.g.* Bailleul *et al.* 2007; Ribic *et al.* 2008; Scheffer *et al.* 2012). Importantly, these programs have revealed habitat overlap between multiple species, which are regarded as areas of ecological significance in the Southern Ocean that can be used for conservation and management purposes (Hindell *et al.* 2011; Raymond *et al.* 2014).

The tracking of subantarctic seabirds and seals has revealed the significance of the ACC fronts and meso-scale oceanographic features to their foraging activity (Bost *et al.* 2009). These species are capable of travelling long distances from their breeding colonies (*e.g.* Kerguelen and Macquarie islands) to reach the SAF (*e.g.* subantarctic fur seals *Arctocephalus tropicalis*), the PF (*e.g.* Macaroni, Royal and King penguins (*Aptenodytes patagonicus*), albatrosses, petrels, Antarctic fur seals and SES) as well as the meso-scale

eddies associated with the fronts (*i.e.* King penguins and SES) (Bost *et al.* 2009). These structures are associated with local upwelling of nutrient-enriched waters, increased productivity and biomass of zooplankton. Myctophid fish often aggregate in and around these structures, which in turn are consumed by top predators (Bost *et al.* 2009).

Closer to the Antarctic continent, numerous studies have shown the importance of the ice-edge habitat, the marginal ice zone (MIZ) as well as the shelf break region or the Antarctic slope fronts (ASF) for top predator species from both the sub-Antarctic colonies and Antarctica (flighted seabirds, penguins, whales and seals) (Chapman *et al.* 2004; Ribic *et al.* 2008; Bost *et al.* 2009; Massom & Stammerjohn 2010). Upwelling MCDW along the continental slopes greatly increases local marine productivity (Prézelin *et al.* 2000; Ducklow *et al.* 2007; Bost *et al.* 2009). In addition to higher biomass, turbulence and frontal structures also concentrate prey, such as the Antarctic krill, which are key to top predator resource acquisition (Bost *et al.* 2009 and reference therein). For example, the circumpolar distribution of whales (*e.g.* blue whales *Balaenoptera musculus*, humpback whales *Magaptera novaeangliae*, fin whales *B. physalus* and minke whales) is tightly associated with the sea-ice extent, itself bounded to the north by the SB-ACC, which reflects the distribution of their main prey: the Antarctic krill (Tynan 1998; Nicol *et al.* 2000).

The topography of the continental Antarctic shelf, via its influence on local hydrology and marine productivity, is also a major driver of top predator habitat selection (Burns *et al.* 2004; Chapman *et al.* 2004; Ribic *et al.* 2008; Raymond *et al.* 2014). At smaller scales, several species adapt their foraging behaviour to favour specific water masses (*e.g.* MCDW) or features within the water column (*e.g.* thermocline) (Charrassin & Bost 2001; Plötz *et al.* 2001; Muelbert *et al.* 2013).

Sea-ice obligate species (*e.g.* Adélie and Emperor penguins, snow petrel, crabeater, leopard, Ross and Weddell seals) are found year-round in association with sea-ice (Tynan *et al.* 2009). As described earlier (see "sea-ice dependant pelagic ecosystem" section) the sea-ice habitat is particularly productive and is associated with important prey for top predators. Within the sea-ice environment, recurring polynyas (*i.e.* persist at the same location over multiple years) have been identified as a major habitat for Antarctic top predators (Tynan *et al.* 2009; Raymond *et al.* 2014). Access to these polynyas in particular drives the life history patterns of several species. For instance, the locations of polynyas affect nesting colonies of Emperor penguins during winter, and Adélie penguin colonies during summer (Ancel *et al.* 1992; Tynan *et al.* 2009). In autumn, the presence of latent heat polynyas is used by Adélie penguins to reach the pack-ice zone before winter. During winter, overwintering or migrating species can depend on them for food and breathing holes (Tynan *et al.* 2009). Polynyas are areas of increased productivity and food availability including diving predator access to under-ice prey (*e.g.* ice krill and silverfish) (McMahon *et al.* 2002; Arrigo & Van Dijken 2003; Tynan *et al.* 2009).

Studies mentioned thus far suggest that predators respond to physical cues to locate favourable habitat and search for prey within (Fauchald & Tveraa 2006; Bost *et al.* 2009)**. Top predators appear to forage equally on prey advected by physical processes and increased local productivity** (Bost *et al.* 2009)**. Thus, any changes in these physical structures could potentially impact the reproductive success and survival of top predators** (Trathan *et al.* 2007; Siniff *et al.* 2008)**.** For instance, the warming trend observed in the Southern Ocean is expected to induce latitudinal shifts of fronts (Moore *et al.* 1999). A southward shift of the PF could induce a shift in foraging areas of several apex predators (*e.g.* Albatrosses, petrels, king penguins, SES, Antarctic fur seals), necessitating greater distances travelled (and therefore increased cost of travel) from

their subantarctic breeding colonies to their foraging grounds. This could ultimately result in a population decline in these species (Inchausti *et al.* 2003; Le Bohec *et al.* 2008). Similarly, variations in sea-ice extent, seasonal persistence and thickness are likely to impact top predators, in particular, sea-ice obligate species which have all their life history traits tightly linked to sea-ice dynamics (Tynan 1998; Siniff *et al.* 2008; Massom & Stammerjohn 2010). Contrasting trends and impacts of sea-ice conditions have been observed and are predicted depending on the region and the species considered (cetaceans, Nicol *et al.* 2008; seals, Siniff *et al.* 2008; seabirds, Jenouvrier *et al.* 2012; Jenouvrier 2013). **This demonstrates why it is vital that researchers continue to study the influence of environmental parameters on the foraging behaviour (*i.e.* a determinant life history trait) of top predators, at a species-regional scale, at several locations around Antarctica.**

D - The Weddell seal

The Weddell seal is the only Antarctic marine mammal remaining in the fast-ice coastal area throughout the year (Burns & Kooyman 2001). They rely on sea-ice for all their life history traits (*i.e.* foraging, breeding, resting) and therefore represents a unique model to improve our understanding of the ecology and adaptation abilities of top predators to the Antarctic extreme environment. The life of the Weddell seal during spring and summer, when they breed and moult in human accessible parts of the fast-ice, is well known (Kooyman 1981). However, Antarctic winter is a critical stage in the life cycle of Weddell seals as it precedes the breeding season and coincides with the female gestation period (Kooyman 1981). Thus, during winter Weddell seals must select favourable habitat and adapt their foraging strategies in order to maximise prey acquisition to ensure their reproductive success. Despite the significance of winter to Weddell seal life history traits, few studies have investigated their movement patterns and diving behaviour during autumn and winter. Most of these studies were conducted at McMurdo sound (Kooyman 1968; Castellini *et al.* 1992a; Testa 1994a; Burns *et al.* 1999) while five others investigated the movement patterns and haul out behaviour of Weddell seals in Prydz Bay (Lake *et al.* 1997, 2003, 2006; Andrews-Goff 2010; Andrews-Goff *et al.* 2010). However, no study to our knowledge has yet related Weddell seals' foraging behaviour to their winter environment. **The aim of this PhD was therefore to improve our understanding of Weddell seals' winter ecology and the foraging strategies they adopt during winter.**

Paper 1

Book chapter (2 p.) in *Atlas des mammifères marins de France et d'Outre Mer* (In press), Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris

(Translated from French – See Appendix A for French version)

The Weddell seal

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E - Context, objectives and thesis outline

The previous sections have demonstrated that the Antarctic environment in winter is associated with complex topographic and hydrological features as well as sea-ice conditions (*e.g.* extent, seasonal persistence, thickness) that regionally affect prey distribution and availability. In addition, winter is associated with decreased productivity due to limited sunlight hours and challenging weather conditions (*e.g.* falling air temperature, strengthening winds, increased ice cover). These environmental conditions directly and indirectly influence the foraging behaviour of top predators (via prey abundance and availability), which ultimately impact their reproductive success and survival. The Weddell seal is a top predator that has all is life history traits tightly linked to sea-ice. Moreover, maximizing their foraging success during Antarctic winter is crucial for their survival and breeding success.

In light of the Antarctic winter environment and the Weddell seal life history traits, the main objective of this PhD was to investigate **the foraging strategies adopted by Weddell seals during winter and discussing likely reasons for these observed strategies.** This main objective called for two sub-objectives:

1. **How can we accurately identify and quantify foraging effort in both the vertical and horizontal dimensions?**

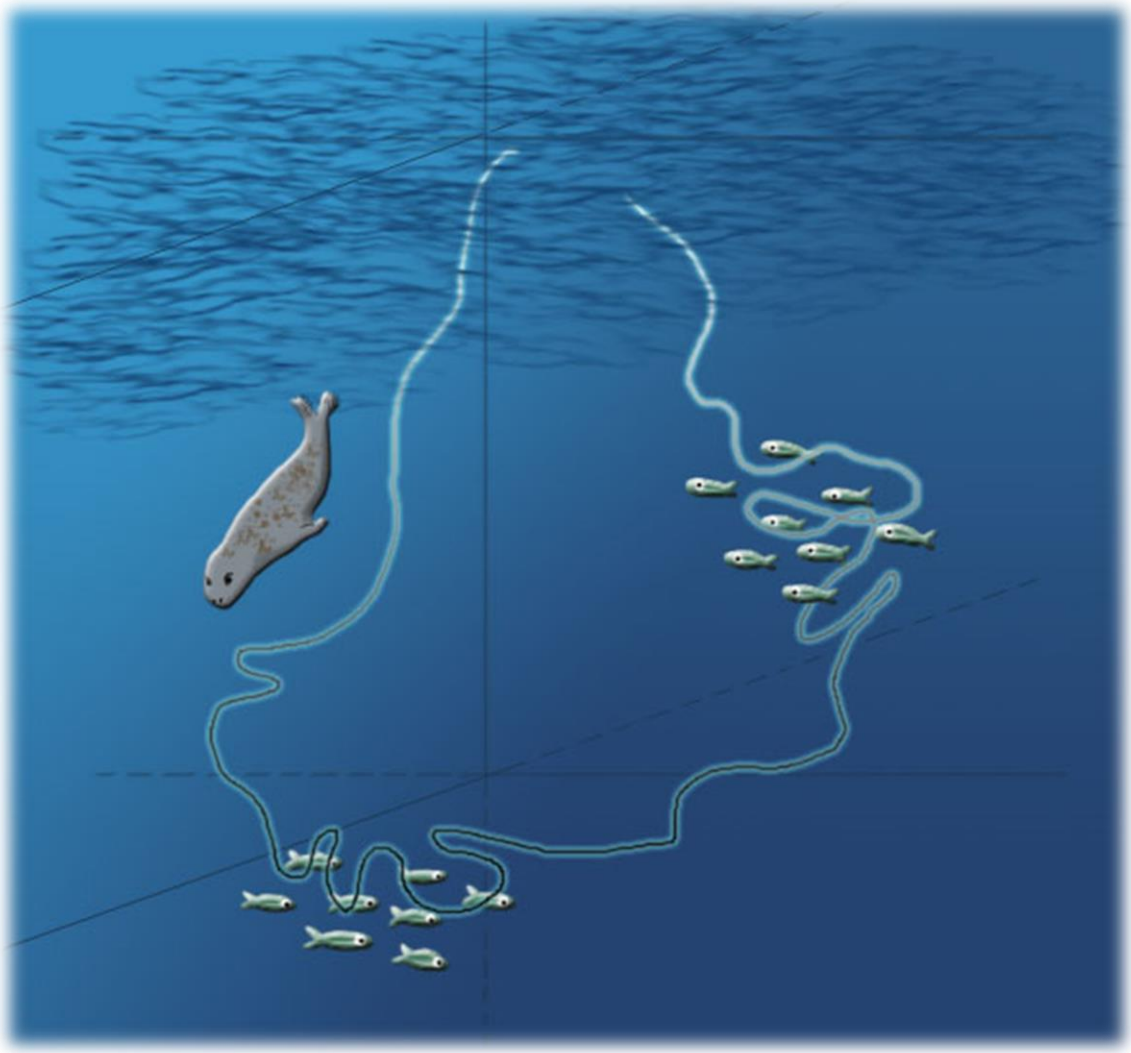
2. **How Weddell seals adapt their behaviour to their environment? And which environmental parameters influence Weddell seals' winter foraging behaviour?**

The thesis is structured so that each of the chapters in part II and III are independent scientific articles that have either already been published (Paper 2 and 4), submitted (Paper 3) or in preparation for publishing (Paper 5). In terms of chronological order, paper 4 was written first as the PhD began by studying the habitat use of Weddell seals from Dumont D'Urville. The next study used high-resolution dive datasets to develop a method allowing the accurate detection of foraging events within the complex dive behaviour of Weddell seals (Paper 3). Because most data collected by focal Weddell seals was recorded at low resolution it was necessary to adapt the method of foraging detection to low-resolution dives (Paper 4). The low-resolution foraging effort metric developed in paper 4 was integrated into a larger habitat use study that used Weddell seal data from the two focal colonies of East Antarctica (*i.e.* Davis and Dumont D'Urville) (Paper 5). However, papers have been grouped according to the questions to be answered in this thesis.

Paper 2 and 3 focused on our first sub-objective and were grouped in the "Methodological challenges" section of this thesis (Part II). The aim of paper 4 and 5 were to answer our second sub-objective and were therefore grouped in the "Weddell seal winter habitat use" section (Part III). An objectives summary and the main findings of each chapter are provided at the beginning and end of each part respectively. Finally, the results of the four research chapters will be integrated and discussed in the last section of the thesis (part IV).

PART II

METHODOLOGICAL DEVELOPMENTS



Dessin de Coralie Chorin

A - Introduction

The aims of the following two chapters were to (i) accurately identify and quantify foraging effort in Weddell seals' dives when only time-depth data are available and (ii) to find suitable methods according to the resolution of the datasets (*i.e.* high resolution vs low-resolution dive profiles).

Common dive analyses are based on the assumption that diving predators maximize their foraging strategy by increasing the time at the maximum depth of their dive while minimizing the time spent in transit (Houston & Carbone 1992; Thompson *et al.* 1993; Schreer *et al.* 2001). Therefore, dives are commonly divided into three phases: the descent, bottom and ascent phases with foraging assumed to occur during the bottom phase (Le Boeuf *et al.* 1988; Hindell *et al.* 1991; Dragon *et al.* 2012a). However, the preliminary analysis of Weddell seal's high-resolution dives (depth recorded every second) revealed a greater complexity in diving behaviour. Indeed, single dives presented several parts where wiggles occurred (*i.e.* vertical sinuosity) and associated with decreased vertical rate of depth changes. This suggested that similarly to the horizontal dimension, a diving predator would exhibit vertical area restricted search (ARS) behaviour (*i.e.* increase of vertical sinuosity and decrease of vertical velocity) in order to increase its time at depths where prey are aggregated. This assumption is also supported by other studies showing that feeding events for different species of marine predators (*e.g.* penguins, seals and whales) were associated with the occurrence of wiggles (*i.e.* vertical sinuosity) (Simeone & Wilson 2003; Goldbogen *et al.* 2006; Bost *et al.* 2007; Calambokidis *et al.* 2007; Hanuise *et al.* 2010 p. 20; Watanabe & Takahashi 2013b). Thus, instead of inferring foraging activity by only considering pre-determined parts of a dive (*i.e.* bottom phase), we aimed to develop a method depicting vertical ARS behaviour along a whole dive profile. Developing this

method should allow detection and quantification of foraging effort within a dive, even for marine predators that display complex diving behaviour (such as the Weddell seal).

The first paper of this section (Paper 2) presents the development of a new method to identify phases within a dive where seals exhibited foraging behaviour. The method was first developed on high-resolution dives recorded with a Time Depth Recorder for a Weddell seal during a whole winter. A complementary dataset of high resolution dives recorded for two southern elephant seals (SES) that travelled in Antarctica during their post-breeding foraging trip was used to test the applicability of the method to other species. Moreover, the concurrent prey capture attempts estimated from high-resolution acceleration (recorded at 16 Hz from a head mounted accelerometer) for SES were independently used to validate the method.

The second paper of this part (Paper 3) aimed to adapt the method developed for high-resolution dives to low-resolution dives. The method developed in Paper 2 relies on the identification of vertical ARS by calculating an index of vertical sinuosity within each part of the dive. However, the dive profiles collected and transmitted by Satellite Relayed Data Loggers (SRDLs) are in a highly degraded form for which the calculation of vertical sinuosity is not possible. These low-resolution dive profiles represent the major part of our dataset for the Weddell seals from Davis and Dumont D'Urville. Indeed, many scientific animal-tagging programs have recorded millions of low-resolution dive profiles in the last decade for several species of marine predators. Thus, it was necessary to find a low-resolution foraging metric which would (similar to a vertical sinuosity index calculated from high-resolution data) allow the detection and quantification of foraging effort within dives.

B - Paper 2

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A new method to quantify within dive foraging behaviour in marine predators

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1. Abstract

Studies on diving behaviour classically divide a dive into three phases: the descent, bottom and ascent phases, with foraging assumed to occur during the bottom phase. The greater complexity of dive revealed through modern, high resolution data highlights the need to re-assess this approach and to consider a larger number of phases within individual dives. Two southern elephant seals (SES) were fitted with a head mounted Time Depth Recorder (TDR) and an accelerometer from which prey capture attempts were estimated. A Weddell seal was also fitted with a TDR. TDRs for both species recorded depth once per second. We quantified the within dive behaviour using an automated broken stick algorithm identifying the optimal number of segments within each dive. The vertical sinuosity of the segments was used to infer two types of behaviours, with highly sinuous segments indicating "hunting" and less sinuous segments indicating "transiting". Using the broken stick method the seals alternated between "hunting" and "transit" modes with an average of 6 ± 2 and 7 ± 0.02 behavioural phases within each dive for the Weddell seal and SES, respectively. In SES, 77 % of prey capture attempts (identified from the acceleration data) occurred in highly sinuous phases (“hunting”) as defined by our new approach. SES spent more time in transit mode within a dive, and hunting mostly occurred during the bottom phase. Conversely the Weddell seal spent more time in hunting mode which also occurred during bottom phase but occurred mostly at shallower depths. Such differences probably reflect different foraging tactics and habitat use. For both species, hunting time differs significantly from bottom time previously used as a proxy for the time spent foraging in a dive. The hunting time defined by our method therefore provides a more accurate fine-scale description of the seals’ foraging behaviour.

Keywords: pinnipeds, foraging behaviour, Austral winter, time-depth recorder, dive profile, marine ecology.

2. Introduction

Predators maximize resource acquisition by adapting their movement patterns and foraging behaviour to the distribution and density of their prey (Charnov 1976; Fauchald *et al.* 2000; Fauchald & Erikstad 2002). In environments where resources are patchily distributed, such as the open ocean, predators need to compensate the costs associated with travel from one patch to another and pursuing a prey with food intake (MacArthur & Pianka 1966). Thus, predators tend to increase the time spent in the vicinity of recent prey captures by decreasing their displacement speed and increasing their turning frequency (Kareiva & Odell 1987; Fauchald & Tveraa 2003). This behaviour, called Area Restricted Search, (ARS) is frequently observed in free ranging predators in the horizontal dimension (Dragon, et al., 2012).

For many marine predators, prey capture occurs in the water column where prey are aggregated (Fuiman *et al.* 2002; Mitani *et al.* 2003; Watanabe *et al.* 2003), making it necessary to also consider the vertical dimension for these species. Identifying feeding events in the vertical dimension (*i.e.* within dives) is still a challenging issue in marine ecology as direct observations are usually impossible. To optimize their foraging strategy when diving, they should decrease their vertical speed and increase the sinuosity of their movements, making what are effectively vertical ARS as indicted on two dimensional dive profiles (Dragon 2011).

Bio-logging devices measure various parameters of free-ranging animal behaviour providing important information on their diving and foraging that are difficult to observe otherwise (Evans *et al.* 2012). Miniaturization, extended battery life and memory size now mean that Time Depth Recorders (TDRs) collect and store data at very high resolutions (one second or less) and for long periods of time (several months) (Block *et al.* 2011; Evans

et al. 2012), enabling the study of diving behaviour at finer spatial and temporal scales than before (Dragon, et al., 2012; Naito et al., 2013; Scheffer et al., 2012). Several foraging metrics (*e.g.* dive duration, dive depth, descent/ascent rate, bottom time, post dive surface interval) can be calculated from TDR data and are used to classify dives into functional categories (Dragon, et al., 2012; Hindell et al., 1991; Kooyman, 1968; Le Boeuf et al., 1988; Schreer and Testa, 1996; Schreer et al., 2001), but typically they are not systematically associated with direct information on food intake (Horsburgh *et al.* 2008). However, the greater complexity of dives revealed through both high resolution time-depth datasets and three-dimensional diving studies suggest that this method could lead to an over-simplification of diving behaviour (Harcourt *et al.* 2000; Simpkins *et al.* 2001). When a seal is spending some time at a particular depth and travelling up and down while at this depth ("wiggles"), it is displaying vertical ARS, and this has been used as an index of foraging activity (not necessarily including prey capture), with several studies providing independent evidence for this in the form of changes in stomach or oesophageal temperature (Bost *et al.* 2007; Horsburgh *et al.* 2008; Zimmer *et al.* 2010; Dragon *et al.* 2012a; Gallon *et al.* 2012). More recently, accelerometers measuring body acceleration in up to three dimensions (*i.e.* surge, heave and sway observed in movements such as: stroke and rolling) have provided insights into the functionality of dive types and the details of fine-scale foraging (Mitani *et al.* 2003; Gallon *et al.* 2012). Stroke frequency has been used as an index of prey pursuit or feeding success (Ropert-Coudert *et al.* 2006; Sato *et al.* 2008). Recent studies have also shown, that for seals, feeding and capture motions are especially visible in the surging axis when using jaw or head accelerometers (Naito *et al.* 2010; Gallon *et al.* 2012; Watanabe & Takahashi 2013a). Using high resolution dive data in combination with a new approach to detect likely foraging events within a dive can greatly improve what information can be derived from time-depth data.

Southern elephant seals (*Mirounga leonina*, hereafter SES) have a circumpolar distribution and forage extensively across the Southern Ocean (Biuw *et al.* 2007). They are associated with important habitats such as the ice edges and continental shelf and feed mainly on fish and squids (Bailleul *et al.* 2007, 2010a; Cherel *et al.* 2008). They are also very deep divers, diving up to 2000 meters and performing on average 60 dives per day (Hindell *et al.* 1991; McIntyre *et al.* 2011). Recent studies have focused on SES fine-scale diving behaviour providing more accurate inferences on their foraging activity (Dragon *et al.* 2012a; Gallon *et al.* 2012; Thums *et al.* 2013). However, little is known about SES vertical ARS behaviour, which is more likely to respond directly to prey distribution. A detailed analysis of their vertical excursions during dives in association with prey capture attempts and prey distribution has yet not been conducted.

Weddell seals (*Leptonychotes weddellii*) are the most southerly breeding seal and typically inhabit sea-ice during the whole year (Cornet & Jouventin 1980; Castellini *et al.* 1992b). Weddell seals are the second deepest phocid diver in the Southern Ocean after the southern elephant seal, attaining 900 m (Heerah *et al.* 2012). They are opportunistic predators feeding mainly on fish, but also on cephalopods and crustaceans, in proportions that vary according to age, location and season (Lake *et al.* 2003). Weddell seal diving and foraging behaviour has been extensively studied during summer in the Ross Sea and the Weddell Sea (Plötz *et al.* 2001; Naito *et al.* 2010). However, because Weddell seals are opportunistic predators it is difficult to associate only one type of foraging dive to their overall behaviour (Davis *et al.* 2003, 2012).

We used high resolution TDR datasets from two SES that travelled to Antarctica during their post-breeding foraging trip and a high resolution TDR dataset covering six winter months from a Weddell seal to develop a new method for identifying the phases within a dive where the seals exhibited foraging behaviour. The concurrent prey capture

attempts estimated from high resolution acceleration available for the SES were independently used to validate the method. Our method aimed to: (i) describe the vertical structure and complexity of seal dives, (ii) determine within each dive the parts where likely foraging occurs and (iii) compare this method to classical dive analysis approach.

3. Materials and methods

Fieldwork and data collection were undertaken with approval from the University of Tasmania animal ethics committee (permit A8523), and from IPEV (Institut polaire français Paul Emile Victor) and TAAF (Terres Australes et Antarctiques Françaises) animal ethics committee.

3.1 Tagging procedure

Two adult female SES (length: 266 and 255 cm) were captured at Kerguelen Island (49°20' S, 70°20' E) in early November before their post breeding trip. One adult female Weddell seal was captured in February 2008 after its annual moult at Dumont d'Urville (66°40' S, 140°00 E) (length 230 cm). Similar capture and tagging procedures were adopted for both species. The seals were approached by foot and temporarily restrained with a head bag and an intravenous injection of Zoletil (1:1 mixture of tiletamine and zolazepam, 0.5 $mg.kg^{-1}$) was administered (Field *et al.* 2002; Wheatley *et al.* 2006; Andrews-Goff *et al.* 2010). A TDR combined with an accelerometer (TDR Mk 10 X, Wildlife Computers) and a TDR (Mk 10, Wildlife Computers) was head-glued to the SES and to the back of the Weddell seal, respectively, using a two component industrial epoxy (Araldite AW 2101). Seals were observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. The TDRs recorded time and pressure at 1Hz. Acceleration was recorded in the 3 axis at 16 Hz.

3.2 Fine scale analysis of foraging behaviour

3.2.1 Surface offset correction

To account for drift in the pressure transducer accuracy and to identify individual dives, we corrected depths using a customised Zero Offset Correction method. We used a moving window of one hour and considered the modal depth between 20 and -20 meters to represent the true surface (assuming that most of the time in this depth range would represent time on the surface. This depth was then subtracted from all depth values in this interval to provide zero offset corrected depths. Only dives below 15 meters were analysed for the SES, while we defined the Weddell seal's dives as being at least 60 seconds long and four meters deep (60 % of all dives) taking into account the accuracy of the pressure transducer (0.5 meters), the size of the seal and sea ice thickness during winter (2.5 – 3 m, Moline *et al.* 2008). The frequency distribution of the Weddell seal diving depths was bi-modal, with two groups of dive depth separated at 20 m. Dives < 20 m were excluded from further analysis (21 % of dives longer than 60 sec.) as they may indicate non-foraging activities (Testa 1994b). SES performed 3941 and 4254 dives with an average (mean ± SD) of 53 ± 1 (max: 68) and 56 ± 1 (max: 104) dives per day, respectively. The Weddell seal performed 11452 dives deeper than 20 m and longer than one minute with an average of 63 ± 24 (max: 115) dives per day. Standard dive parameters were calculated using classical dive analysis methods (Le Boeuf *et al.* 1988; Hindell *et al.* 1991; Schreer & Testa 1996), dividing each dive into an descent, bottom and ascent phase based on inflection points.

3.2.2 Dive analysis with the optimised and automated broken stick method

As an alternative to the classic three-phases (i.e ascent, bottom and descent) dive analysis (CA) we used a method based on a broken stick algorithm (BS). This method selects the data points where the dive trajectory between two points changes the most rapidly (inflexion points). Any number of points can be chosen depending on the resolution required (Fedak *et al.* 2001). We started with three points: (i) surface start point, (ii) maximal depth and (iii) surface end point (Fig.2.1 A). We then iteratively selected the data points of maximum difference between the original dive profile and the dive profile reconstructed by linear interpolation between the points selected during the previous iterations (Fig.2.1, Script S2.1 and Dataset S2.1).

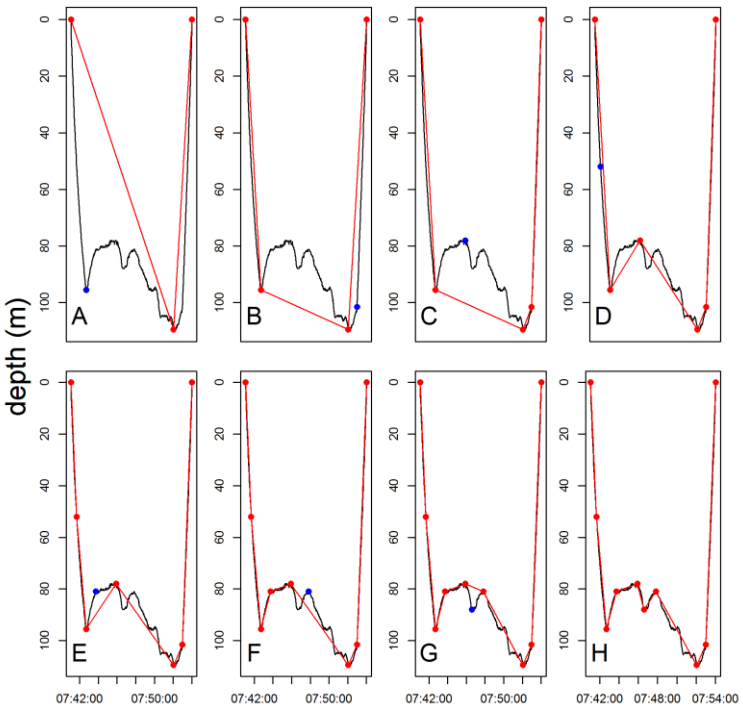

Figure 2.1. The broken stick algorithm. The iterative process of the broken stick algorithm is presented from panel A to H. The broken stick method iteratively selects the data points (in blue) of maximum difference between the original dive profile (black line) and the dive profile reconstructed by linear interpolation (red lines) between the points selected during the previous iterations (in red). A Weddell seal dive was used as an example for this graph.

We then estimated the optimal number of broken stick points (from 6 to 33) that best summarize the dive shape. For this, we calculated a mean distance based on the average of the differences between each data point and its corresponding position on the line between the broken stick points (Fig. 2.1, averaged depth differences between the black curve and the red lines). The mean distance was calculated for each dive summarised with 6 to 33 broken stick points (Fig. 2.2 A, Script S2.1 and Dataset S2.1). For each dive we plotted the mean distance for a range of broken stick points and we determined the inflexion point of this curve (i.e the point after which the amount of new information explained by increasing the number of segments$_{BS}$ began to decline).

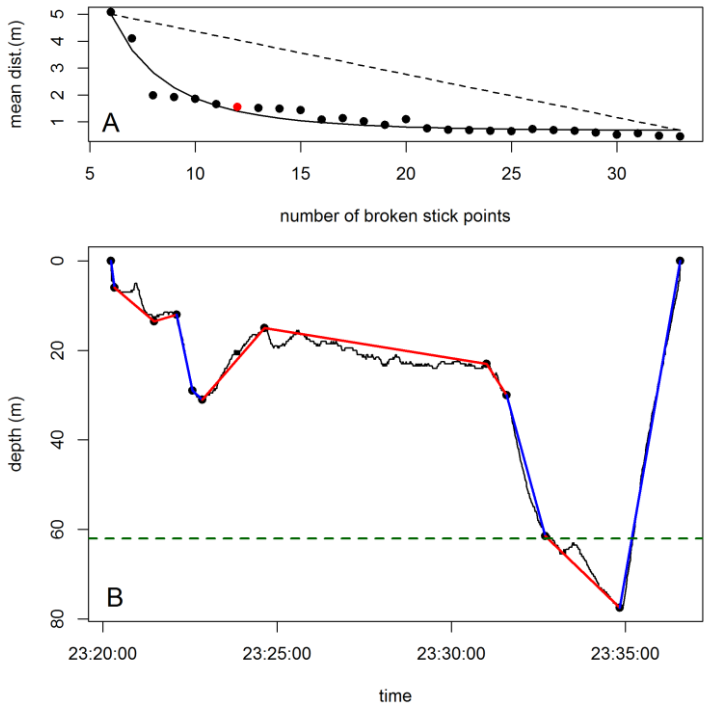

Figure 2.2. Optimization of the broken stick algorithm. Any number of broken stick points can be chosen depending on the resolution required to describe a dive. A: Mean distance according to the number of broken stick points (from 6 to 33) which are used to describe the dive represented below (B). The mean distance is the average of the differences between each data point of the original profile and the corresponding point of the reconstructed profile obtained by linear interpolation between the broken stick points (from 6 to 33). The inflexion point of the mean distance curve (A, red data point) is determined by calculating the maximal distance between the asymptote curve obtained by fitting a Gompertz model to the mean distance (A, black line) and the linear approximation (A, dashed black line) between its start and end points. B: Original dive profile (B, black line) summarized by the optimal number of broken stick points (B, black data points) as estimated by mean distance represented above (A). The blue lines represent transit segmentsBS and the red lines represent hunting segmentsBS. The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. A Weddell seal dive was used as an example for this graph.

To do this in an automated way, each integrated distance curve was smoothed by fitting to a Gompertz model (R Development Core Team 2008). The inflexion point of this curve was then determined by calculating the maximum distance between the Gompertz curve and the linear approximation between its start and end points (Fig. 2.2 A, Script S1 and Dataset S1). The number of corresponding broken stick points was then used to optimally describe each dive (Fig. 2.2, Script S2.1 and Dataset S2.1). There was no trend in the relationship between the mean distance and the number of broken stick points per dive (mean ± SD, 5 ± 0.02 m, min: 0.3 m, max: 18 m and 1.2 ± 0.8 m, min: 0.15 m, max: 7.8 m, for the SES and the Weddell seal respectively) (Fig. 2.3), showing that there is no bias associated with dive complexity.

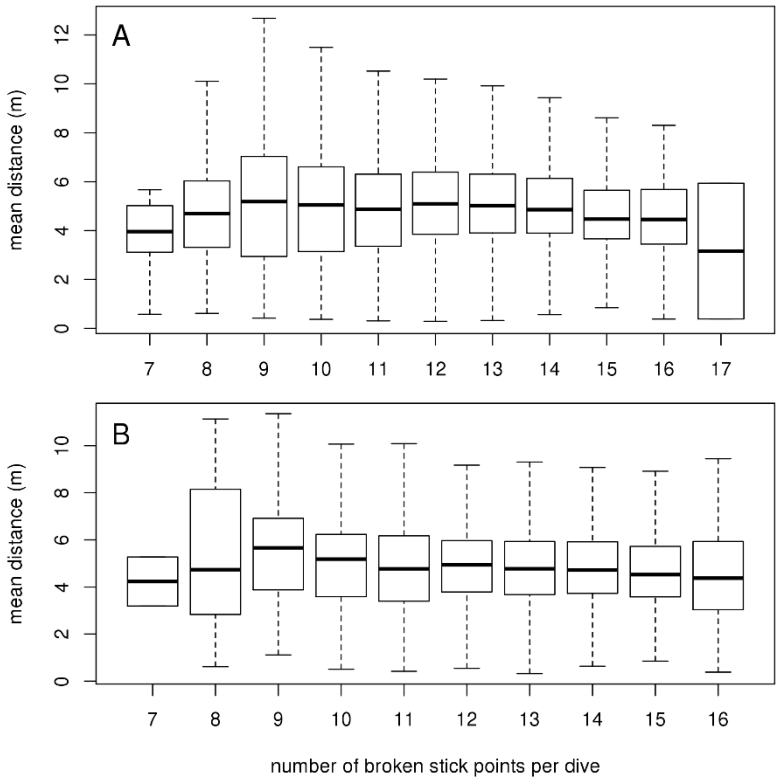

Figure 2.3. Distribution of the mean distance. Distribution of the mean distance (m) according to the optimal number of broken stick points calculated for each dive for the southern elephant seals (A) and the Weddell seal dataset (B). See figure 2.2 for calculation of the optimal number of broken stick points.

3.2.3 Detection of intensive foraging within dives

Based on the definition of Area Restricted Search (ARS) in the horizontal dimension when animals are at the surface (Fauchald & Tveraa 2003), we expected diving predators such as the SES and the Weddell seal to adjust their diving behaviour in order to increase the time spent in a patch of prey, by decreasing their vertical velocity and increasing the vertical sinuosity of their trajectory. Therefore for each segment between two broken stick points (hereafter $segment_{BS}$) we calculated, (i) the vertical descent/ascent rate (in m/s) and (ii) the vertical sinuosity (Script S1 and Dataset S1) adapted from (Dragon *et al.* 2012a) as:

$$Sinuosity = \frac{Dist_{brokenstick}}{Dist_{observed}}$$

where $Dist_{broken\ stick}$ is the vertical distance swum between the two broken stick points considered, and the $Dist_{observed}$ is the sum of all the vertical distances from the original dive profile between the two corresponding depth points. Vertical sinuosity ratio (hereafter sinuosity) takes a value of 1 when the individual swims in a straight path during this part of the dive. Any deviation from a straight path decreases the sinuosity ratio toward 0.

The distribution of the sinuosity index of all dive $segments_{BS}$ and for both species was distinctly bi-modal (sinuosity comprised between 0 and 0.9 and sinuosity >0.9, Fig. 2.4) suggesting two behavioural modes. We used the 0.9 sinuosity threshold to discriminate vertical search $mode_{BS}$ ($0 < sinuosity > 0.9$) from directed travel $mode_{BS}$ ($0.9 \leq sinuosity \geq 1$) within each dive. Hunting $mode_{BS}$ was characterized by a more sinuous path, possibly indicating intra-patch movements, whereas directed travel $mode_{BS}$ showed a straighter path probably occurring during inter-patch movements or when transiting from surface to/from depth.

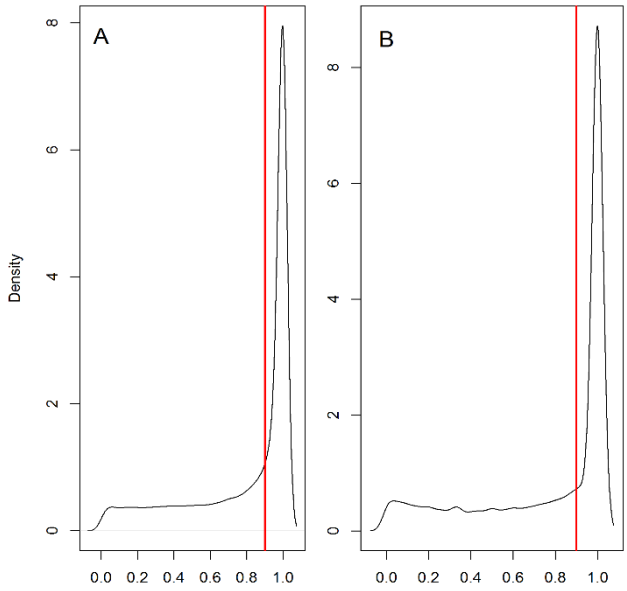

Figure 2.4. A bimodal behaviour. Density plots representing the distribution of the vertical sinuosity calculated for each broken stick segment from the elephant seal dives (A) and the Weddell seal dives (B). The 0.9 sinuosity threshold represented by the vertical red line was used to discriminate "transit" mode$_{BS}$ versus "hunting" mode$_{BS}$.

Successive broken stick segments of the same behavioural mode$_{BS}$ were then grouped in hunting or transiting phases$_{BS}$ allowing us to quantify the phases$_{BS}$ within each dive (Fig. 2.2 B). For each dive, we characterized each phase$_{BS}$ using the behavioural mode$_{BS}$ (i.e. hunting vs transit), the number of broken stick segments making up each phase$_{BS}$, its duration, its mean depth and its mean ascent/descent rate (Script S1 and Dataset S1). For the SES data set, we also counted the number of prey capture attempts that occurred in each behavioural phase$_{BS}$. They were calculated from the concurrent high resolution acceleration data (Viviant *et al.* 2009; Guinet *et al.* 2014). Briefly, acceleration data were used to identify rapid head movements that may be associated with prey encounter events and these are visible as spikes in the filtered acceleration profiles (Gallon *et al.* 2012). Acceleration profiles with more than one spike above a given threshold (in m/s^2) visible both in the surge and heave axes were considered to be related to prey encounter events. A full description of the acceleration data filtration process and definition of the threshold for the spike occurrence are given in (Gallon *et al.* 2012) and (Guinet *et al.* 2014).

3.2.4 Comparison of the two behavioural modes$_{BS}$

In the Weddell seal data set a number of segments$_{BS}$ showed very high vertical ascent/descent rates, which may result from depth measurement errors by the sensor. Davis *et al.* (2012) used a velocity sensor recording swimming speed and observed mean maximum speeds up to 5.1 ± 1 m/s depending on the type of dive and location. We therefore removed dives containing segments$_{BS}$ with ascent/descent rates > 7 m/s (23 dives in the Weddell seal dataset). In SES the maximum ascent/descent rates of the broken stick segments was 3.5 m/s, therefore all the SES dives were retained.

We compared the number of prey capture attempts (when available), duration, depth, and ascent and descent rates between the two behavioural modes$_{BS}$ estimated with our method (i.e. hunting vs transit) using unilateral Welch tests on two datasets of 10 % of the dives randomly selected for each behaviour. We also compared the time spent in hunting mode$_{BS}$ with the bottom time$_{CA}$ identified in the classical method, using unilateral Welch tests on two datasets of 10 % of total dives randomly selected (R Development Core Team 2008; Millot 2011). The Welch test allows comparing samples with different variances. “Unilateral” means that we tested if the mean of one sample was significantly greater than the other one (Millot 2011).

4. Results

4.1 General diving behaviour

The TDRs recorded the diving behaviour of two southern elephant seals for 72 and 73 days from early November to January 2010 (Table 2.1). The seals performed 3941 and 4254 dives with an average (mean ± SD) of 53 ± 1 and 56 ± 1 dives per day, respectively (Table 2.1). The mean maximum dive depths were 511 ± 4 m and 475 ± 4 m with average dive durations of 23 ± 0.01 min and 21 ± 0. 1 min, respectively (Table 2.1).

The diving behaviour of the Weddell seal was recorded for 182 days from late February to late August 2008 (Table 2.1). The seal performed 11452 dives deeper than 20 m and longer than one minute with an average of 63 ± 24 dives per day (Table 2.1). The mean maximum dive depths were 67 ± 54 m with average dive durations of 10 ± 6 min (Table 2.1).

Table 2.1. General information on tag transmission and diving behaviour. Data are given for two adult female southern elephant seals (SES) captured at Kerguelen Island (49°20' S, 70°20' E) and one adult female Weddell seal captured at Dumont d'Urville (66°40' S, 140°00 E). Both species were fitted with TDRs. Accelerometers were also head-mounted on SES.

	Tag deployment	Tag retrieval	Transmission duration (days)	Number of dives	Number of dives per day	Dive maximum depth (m)	Dive duration (min)
SES 1	2010-10-31	2011-01-21	72	3941	53 ± 1 max: 68	511 ± 4 max: 1260	23 ± 0.01 max: 56
SES 2	2010-01-11	2011-01-15	73	4254	56 ± 1 max: 104	475 ± 4 max: 1296	21 ± 0. 1 max: 50
Weddell seal	2003-02-23	2008-10-20	182	11452	63 ± 24 max: 115	67 ± 54 max: 645	10 ± 6 max: 46

4.2 Foraging behaviour

4.2.1 Comparison between the broken stick analysis and prey capture attempts in SES

Dives included an average of 12 ± 0.02 (max: 16, SES 1), 12 ± 0.02 (max: 17, SES 2) and 12 ± 2 (max: 17, Weddell seal) broken stick segments using the broken stick algorithm. However, the fit of the Gompertz model included in the method did not work for 6 % of the SES dives and 4 % of the Weddell seal dives which were removed from the dataset. For these dives, the relationship between the mean distance and the number of broken stick points was more linear (Fig. S2.1). Consequently, the model could not detect an inflexion point, which is necessary for determining the optimal number of broken stick points needed to summarize the dive (Fig. S2.1). In these cases, the number of broken stick points can be determined subjectively by the user (e.g could be determined to suit the averaged mean distance for all dives).

SES dives were rarely associated with more than 40 prey capture attempts, therefore these dives with > 40 prey capture attempts were also removed from the dataset (0.1 % of the SES dives). Of the remaining SES dives, there were 1369 dives that were not associated with prey capture attempts (17 % of the SES dives) but during which the SES spent 8 ± 13 min in hunting mode$_{BS}$. These dives were, on average, 393 ± 6 m deep, 20 ± 2 min long and characterized by 5 ± 0.05 behavioural phases$_{BS}$. The remaining dives (6814) were associated with an average of 11 ± 0.1 prey capture attempts and on average 9 ± 0.05 min were spent in hunting mode$_{BS}$. Foraging dives (dives with >0 prey capture attempts) were on average 512 ± 3 m deep, 22 ± 0.05 min long and characterized by 7 ± 0.02 behavioural phases$_{BS}$. Dives with prey capture attempts were significantly deeper, longer, more complex (as they were characterized by more behavioural phases$_{BS}$) and more time was spent in hunting mode$_{BS}$ than dives without prey capture attempts (Table 2.2).

Table 2.2. Comparison of dives with or without prey capture attempts as inferred from acceleration data in southern elephant seals. Duration, depth, complexity (number of behavioural phasesBS) and time spent in hunting modeBS for 1000 dives randomly selected that are associated (w) or not (w/o) with prey capture attempts (PrCA) were compared using unilateral Welch tests.

	Dives w/o PrCA	Dives w PrCA	t	df	p-value
Depth (m)	394 ± 7	514 ± 7	12	1998	< 0.001
Duration (min)	21 ± 0.2	22 ± 0.14	5.3	1765	< 0.001
Number of behavioural phases$_{BS}$	5 ± 0.06	7 ± 0.06	23	1998	< 0.001
Time spent in hunting mode$_{BS}$ (min)	8 ± 0.15	9 ± 0.1	4	1974	< 0.001

Table 2.3. Comparison of within dive behavioural modesBS in southern elephant seals and Weddell seal. Duration, depth, absolute values of ascent and descent rates (mean ± se) and the number of prey captures attempts (SES) between the two foraging modesBS were compared using unilateral Welch tests for two independent sets of 10 % of the total dives randomly selected for each modesBS. SES stands for southern elephant seals.

	Species	Hunting mode$_{BS}$	Transit mode$_{BS}$	t	df	p-value
Depth (m)	SES	386 ± 4	304 ± 3	15	5363	< 0.001
	Weddell seal	49 ± 0.9	38 ± 0.6	9.9	5567	< 0.001
Duration (min)	SES	2.8 ± 3	2.9 ± 3	1.9	5604	< 0.05
	Weddell seal	2.5 ± 3.4	0.9 ± 0.9	27	3314	< 0.001
Ascent/descent rate (m.s^{-1})	SES	0.3 ± 0.004	1.23 ± 0.006	126	9153	< 0.001
	Weddell seal	0.13 ± 0.001	1.2 ± 0.01	72	7842	< 0.001
Number of prey capture attempts	SES	2.5 ± 0.07	0.6 ± 0.02	27	3047	< 0.001

Hunting phases$_{BS}$ (defined by the broken stick method) of the SES foraging dives were associated with four times more prey capture attempts than transit phases$_{BS}$ (hunting mode$_{BS}$: 2.5 ± 0.02, transit mode$_{BS}$: 0.6 ± 0.007; Table 2.3, Fig. 2.5). Of the total prey capture attempts, 77 % and 23 % occurred during hunting and transit phases$_{BS}$, respectively.

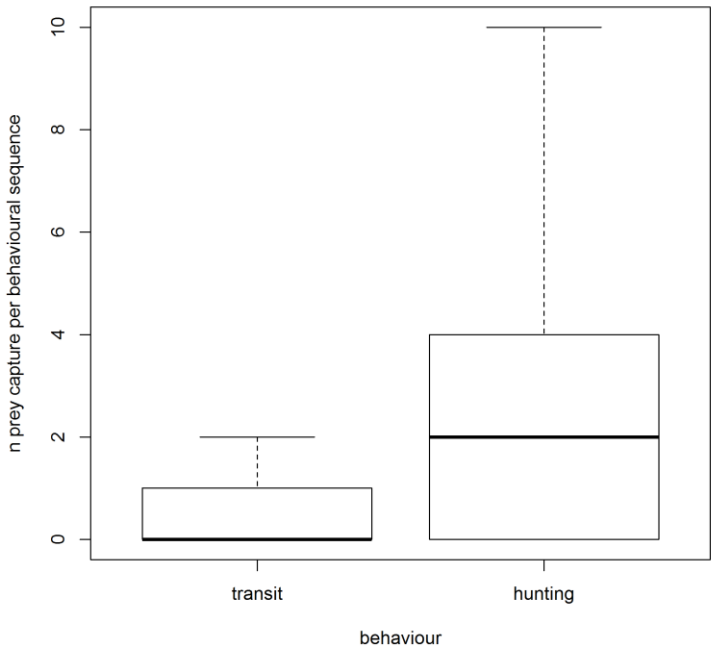

Figure 2.5. Behavioural differences in prey capture attempts in SES. Distribution of the number of prey capture attempts calculated for each segments$_{BS}$ according to transit mode$_{BS}$ and hunting mode$_{BS}$, respectively for the elephant seal foraging dives.

4.2.2 Comparison of behavioural modes$_{BS}$ defined by the broken stick analysis

Within dive behaviour was characterized by two behavioural modes$_{BS}$: (i) hunting and (ii) transit mode$_{BS}$ (Fig. 2.1, 2.6 and 2.7). On average, dives were summarized by 7 ± 0.03 (max: 15, SES 1), 7 ± 0.03 (max: 13, SES 2) and 6 ± 2 (max: 13, Weddell seal) behavioural phases$_{BS}$.

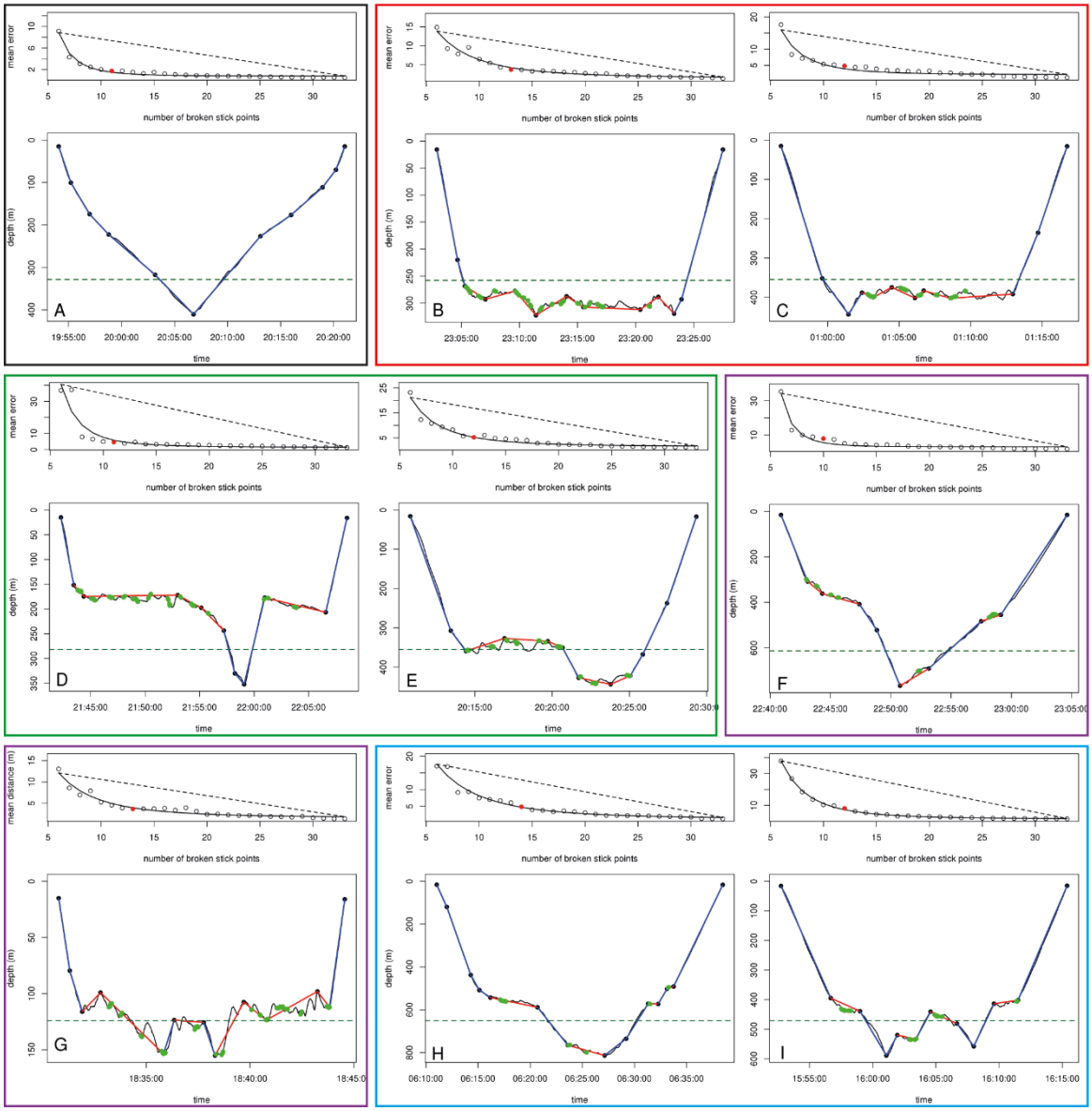

Figure 2.6. Complexity of the dives for the southern elephant seals. For each panel, the top graph represents the mean distance according to the number of broken stick points in order to select the optimal number of broken stick points to best describe each dive. See figure 2.2.A for a full description. The lower graph of each panel represents the original dive profile (black line) summarized by the optimal number of broken stick points (black data points). The blue lines represent transit segmentsBS, the red lines represent hunting segmentsBS and the green dots indicate prey capture attempts (estimated from acceleration data). The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. Figures are represented from A to I, from the simplest to the most complex dives, with zero (A, grey frame) to four (H and I, blue frame) hunting phasesBS.

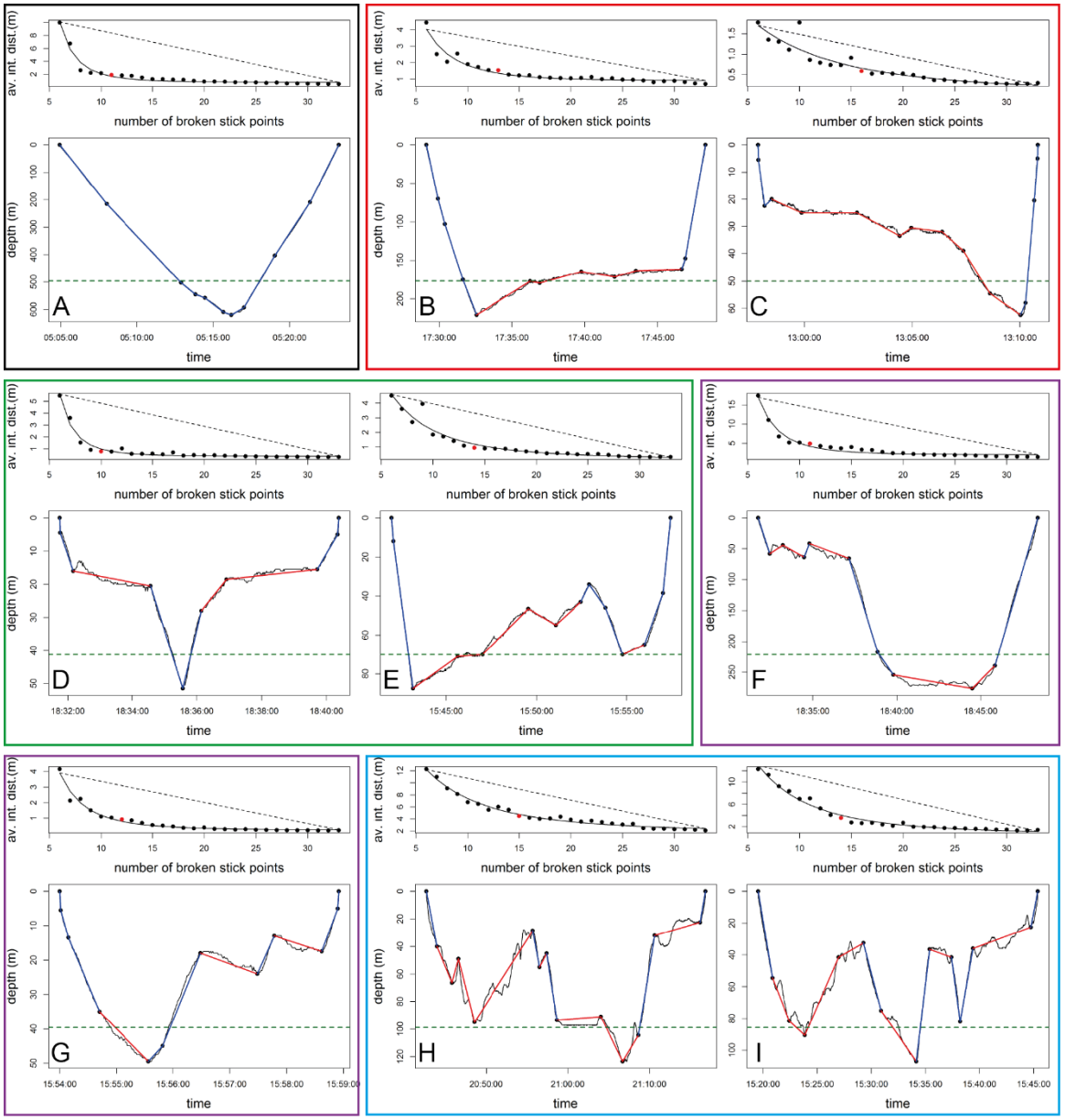

Figure 2.7. Complexity of the dives for the Weddell seal. For each panel, the top graph represents the mean distance according to the number of broken stick points in order to select the optimal number of broken stick points to best describe each dive. See figure 2.2.A for a full description. The lower graph of each panel represents the original dive profile (black line) summarized by the optimal number of broken stick points (black data points). The blue lines represent transit segmentsBS and the red lines represent hunting segmentsBS. The green dashed line represents the depth below which bottom time is calculated with the classical dive analysis method. Figures are represented from A to I, from the simplest to the most complex dives, with zero (A, grey frame) to four (H and I, blue frame) hunting phasesBS.

This provides considerably more detail than the simple three phases$_{CA}$ (descent, bottom and ascent phases$_{CA}$) found with the classic dive analysis method (Fig.2.6 and 2.7). For the SES, dives with three hunting phases$_{BS}$ were the most frequent (35 % of all dives, Fig.2.8 a and Fig.2.6 f-g), followed by those with two (Fig.2.6 d-e), four (Fig.2.6 h-i) and one (Fig.2.6 b-c) hunting phases$_{BS}$ representing, 25 %, 24 % and 9 % of all dives, respectively (Fig. 2.8 a). Dives with five, six, zero (Fig.2.8 a) and seven hunting phases$_{BS}$ were scarce, representing 6 to 0.2 % of the dives, respectively (Fig. 2.8 a). Weddell seal's dives with two hunting phases$_{BS}$ were the most frequent (36 % of all dives, Fig. 2.8 b and Fig.2.7 d-e), followed by those with three (Fig.2.7 f-g), one (Fig.2.7 b-c) and four (Fig.2.7 h-i) hunting phases$_{BS}$ representing, 28 %, 20 % and 11 % of all dives, respectively (Fig. 2.8 b). Dives with five, zero (Fig.2.7 a) and six hunting phases$_{BS}$ were scarce, representing 2.7 to 0.2 % of the dives, respectively (Fig. 2.8 b).

SES hunting phases$_{BS}$ were deeper than transit phases$_{BS}$ as they were localized at 80 ± 0.12 % (393 ± 1 m) and 64 ± 0.12 % (312 ± 1 m) of the maximal dive depth, respectively (Table 2.3, Fig. 2.9 b). Hunting phases$_{BS}$ were shorter than transit phases$_{BS}$ representing 14 ± 0.1 % (3 ± 0.01 min) and 15 ± 0.1 % (3.3 ± 0.01 min) of the dive duration, respectively (Table 2.3, Fig. 2.9 a). When displaying hunting behaviour, SES decreased their instantaneous vertical velocity compared to the one adopted during transit behaviour (hunting mode$_{BS}$: 0.3 ± 0.001, transit mode$_{BS}$: 1.22 ± 0.002; Table 2.3, Fig. 2.10 a).

The Weddell seal hunting phases$_{BS}$ were deeper than transit phases$_{BS}$ as they were localized at 66 ± 26 % (47 ± 45 m) and 51 ± 23 % (36 ± 35 m) of the maximal dive depth, respectively (Table 2.3, Fig. 2.9 b). Hunting phases$_{BS}$ were also longer than transit phases$_{BS}$ representing 25 ± 23 % (3 ± 3 min) and 12 ± 14 % (1 ± 1 min) of the dive duration, respectively (Table 2.3, Fig. 2.9 c). The Weddell seal decreased its instantaneous vertical

velocity during hunting mode$_{BS}$ compared to the one adopted during transit behaviour (hunting mode$_{BS}$: 0.13 ± 0.13 m/s, transit mode$_{BS}$: 1.3 ± 1.9 m/s; Table 2.3, Fig. 2.10 b).

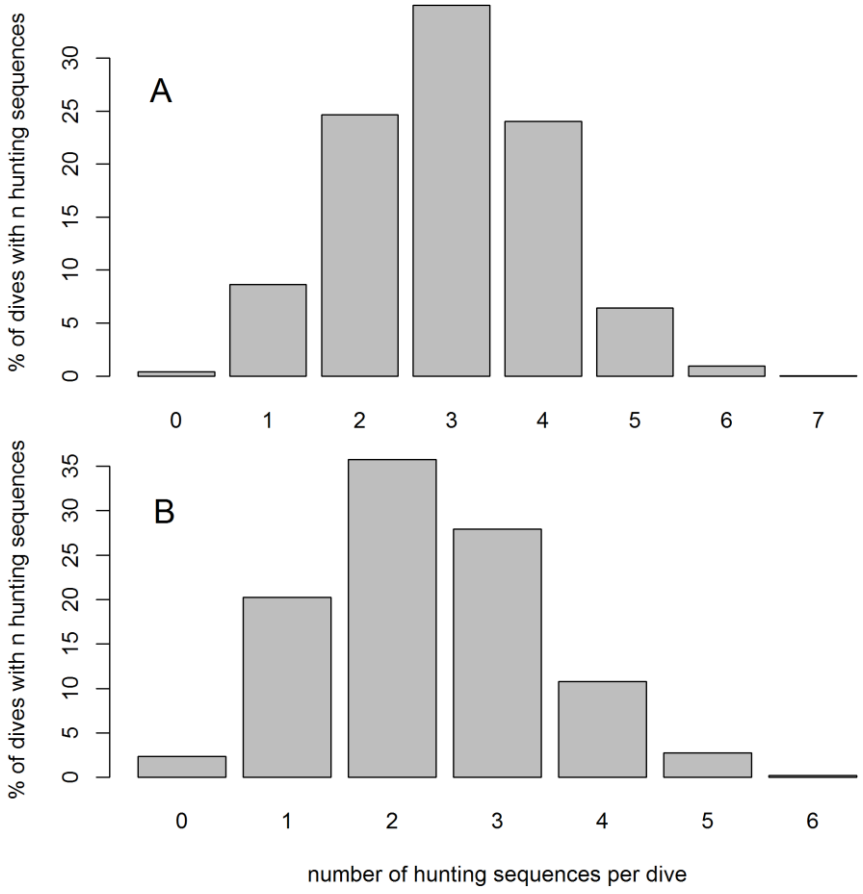

Figure 2.8. Occurrence of hunting modeBS. Proportion of dives containing from zero to seven hunting phasesBS (%) for the southern elephant seals (A) and the Weddell seal (B).

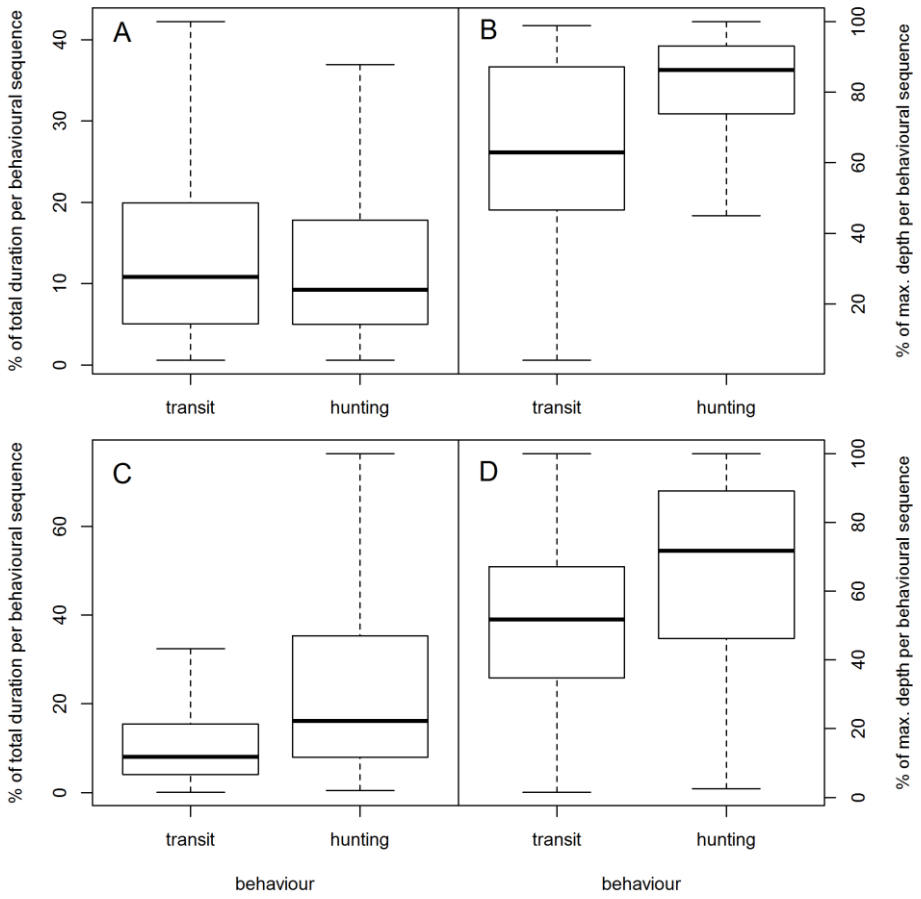

Figure 2.9. Behavioural modeBS differences. Distribution of each behavioural phaseBS duration (sec.) expressed in percentage of the corresponding dive total duration (sec.) for transit modeBS and hunting modeBS, respectively (A: southern elephant seals, C: Weddell seal). Distribution of each behavioural phaseBS depth (m) expressed in percentage of the corresponding dive maximal depth (m) for each of the two modesBS (B: southern elephant seals, D: Weddell seal). The horizontal bold line of the box shows the median. The bottom and top of the box show the 25th and 75th percentiles.

4.2.3 Comparison between the Broken stick and the Classical dive analysis

The SES spent 41 % and 59 % of their total time foraging when considering the sum of time spent in hunting $mode_{BS}$ and bottom $time_{CA}$ for all dives, respectively. The mean bottom $time_{CA}$ per dive calculated from the classical method was 13 ± 0.05 min whereas time spent in hunting $mode_{BS}$ per dive (i.e. the sum of the different hunting $phases_{BS}$ within a dive) was 9 ± 0.05 min, representing 59 ± 0.2 % and 42 ± 0.2 % of the corresponding dive duration, respectively. Statistical comparison on 10 % of the dives,

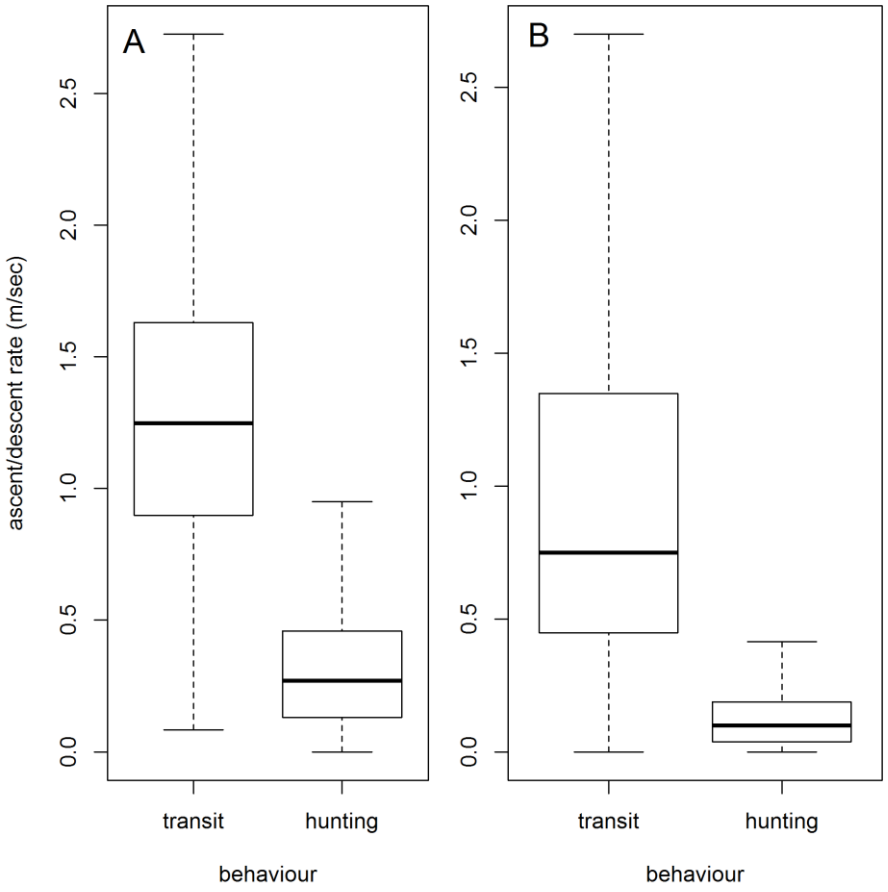

Figure 2.10. Behavioural differences in ascent/descent rates. Distribution of the ascent/descent rates (m.sec-1) calculated for each segmentsBS according to transit modeBS and hunting modeBS, respectively for the southern elephant seals (A) and the Weddell seal (B). The horizontal bold line of the box shows the median. The bottom and top of the box show the 25th and 75th percentiles.

revealed that bottom $time_{CA}$ was significantly longer than time spent in hunting $mode_{BS}$ (Table 2.4). The time spent in transit per dive represented 58 ± 0.2 % of the corresponding dive duration for the BS method compared to 41 ± 0.2 % for the classical approach.

The Weddell seal spent 67 % and 46 % of its total time foraging when considering the sum of time spent in hunting $mode_{BS}$ and bottom $time_{CA}$for all dives, respectively. The mean bottom $time_{CA}$ per dive calculated from the classical method was 4 ± 4 min whereas the time spent in hunting $mode_{BS}$ per dive was 6 ± 5 min, representing 42 ± 26 % and 59 ± 25 % of the corresponding dive duration, respectively. Unlike the SES, the mean bottom

$time_{CA}$ per dive was significantly shorter than the time spent in hunting $mode_{BS}$ per dive (Table 2.4). The time spent in transit represented 41 ± 24 % of the corresponding dive duration for the BS method compared to 58 ± 24 % for the classic approach.

In SES 43 % of the hunting $phases_{BS}$ occurred above the bottom $phase_{CA}$ identified by the classical approach. For the Weddell seal, 61 % hunting $phases_{BS}$ occurred above the bottom $phase_{CA}$ identified by the classical approach (Fig. 2.7).

Table 2.4. Comparison of the broken stick and the classical dive analysis. Duration of the time spent foraging estimated from bottom time (classical dive analysis) and the time spent in hunting modeBS (broken stick method) were compared using unilateral Welch tests for two independent sets of 10 % of the total dives selected randomly for both species. SES stands for southern elephant seals.

	Species	Hunting $mode_{BS}$	Bottom $time_{CA}$	n	t	df	p-value
Duration per dive (min)	SES	9 ± 0.07	13 ± 0.08	818	36	7947	< 0.001
Duration per dive (min)	Weddell seal	6 ± 0.1	4 ± 0.1	1144	12	2197	< 0.001

5. Discussion

In natural systems, predators perceive and react to environmental heterogeneity. These reactions are detected through changes in movement characteristics of animals (*e.g.* direction, speed, sinuosity) (Fauchald & Tveraa 2003; Jonsen *et al.* 2007), that are likely to reflect changes in the presence, or availability, of prey.

We present a new method to quantify the within-dive complexity of diving predators, and demonstrate it using high resolution TDR datasets from two SES and a Weddell seal. We assessed within-dive behavioural $phases_{BS}$ (*e.g.* hunting vs transit) using concepts derived from ARS analyses developed for horizontal track analysis. Our results show: (i) the seals alternated between hunting and transit $modes_{BS}$ at the scale of a dive; (ii) the dives were mainly characterized by numerous behavioural $phases_{BS}$ instead of the three previously described $phases_{CA}$ (descent, bottom and ascent), of which only one (the bottom) was deemed to be involved in foraging; (iii) 77 % of total SES actual prey capture attempts occurred in our identified hunting $mode_{BS}$ and intra-dive hunting $phases_{BS}$ were associated on average with four times more prey capture attempts (SES) than transit $phases_{BS}$; (iv) hunting $mode_{BS}$ was adopted two or three times in a dive and was shorter (SES) or longer (Weddell) than that classically estimated from bottom $time_{CA}$. Even though based on a small sample of individuals, this study demonstrates on two seal species that our simple algorithm represents a powerful tool to identify within a dive the parts where the individual intensify its foraging behaviour.

5.1 Detection of intensive foraging activity within dives

Simple depth and time data give a greatly simplified representation of what are very complex and dynamic 3D behaviours. Nonetheless, they still have provided very valuable

inferences about key ecological parameters such as foraging, at very relevant temporal and spatial scales (Dragon et al., 2012; Hindell et al., 1991; Le Boeuf et al., 1988; Scheffer et al., 2012; Schreer et al., 2001). Our approach was based on the transposition of ARS to the vertical dimension. In the horizontal dimension, ARS is characterized by an increase of the trajectory sinuosity and a decrease of displacement speed (Kareiva & Odell 1987; Fauchald & Tveraa 2003), and is often used as a proxy for intensification of the foraging behaviour (Bailleul *et al.* 2008; Dragon *et al.* 2012a; b; Thums *et al.* 2013). Weimerskirch *et al.* (2007) showed in seabirds, that while food intake could occur outside ARS, it was more predictable in these areas. Here, we identified ARS in the vertical dimension in order to identify those parts of the dive during which the seal increased its foraging activity.

One limit of our study could be that it was based on data from three individuals, though this is compensated to some extent by the very large number of high resolution dives included in the analysis. Nonetheless, two behavioural modes$_{BS}$ were clearly identified in the vertical dimension according to the sinuosity of the dive segments$_{BS}$ identified with the broken stick method.

In our study, 77 % of the SES prey capture attempts measured independently occurred during hunting phases$_{BS}$. Acceleration data cannot discriminate between successful prey capture attempts and unsuccessful ones, thus it doesn't give a true estimation of feeding success. Nonetheless it is a proxy for predators interactions with prey (Viviant *et al.* 2009; Gallon *et al.* 2012) and can provide information on the distribution and abundance of prey in the water column (Plötz *et al.* 2001; Viviant *et al.* 2009; Naito *et al.* 2010, 2013). The remaining 23 % of the SES prey capture attempts occurred during transit phases$_{BS}$ suggesting opportunistic interactions with more dispersed prey resource (Guinet *et al.* 2014). Our results are consistent with transit phases$_{BS}$ representing: (i) transit from the surface to depth of interest or (ii) travel between prey within a dive therefore

corresponding to "exploratory phases". Conversely, the intensification of the seal vertical foraging behaviour can be interpreted as behavioural responses to local increased densities of prey field. During faster, straight transiting parts within the dive, the seal could explore the water column to reach a region occupied by prey. The seal then probably optimizes the time spent in that area by: (i) making "wiggles"; (ii) decreasing its vertical speed and; (iii) horizontally meander at that depth, which cannot be detected with our dataset but which has been previously observed in 3D movements analysis studies (Hindell *et al.* 2002; Davis *et al.* 2003, 2012). Thus, intensive foraging depths likely correspond to the depths where prey patches are located.

Vertical sinuosity (or wiggles) is often used as an index of foraging effort and/or feeding success even when no independent information on prey capture is available (Hindell *et al.* 1991, 2010; Schreer & Testa 1996; Dragon *et al.* 2012b). In our study, non-foraging SES dives were also characterized by some hunting $phases_{BS}$, but they only represented a minority of the dives performed. It is possible that in non-foraging dives SES captured their prey by suction which wouldn't be detected in acceleration data (Viviant *et al.* 2009). Feeding by suction has been previously observed for sea lions, leopard, bearded and hooded seals (Marshall *et al.* 2008; Suzuki *et al.* 2009; Viviant *et al.* 2009; Hocking *et al.* 2013). Most likely vertical sinuosity is also indicative of searching to locate prey, and therefore still reflects an intensification of the foraging effort (Gallon *et al.* 2012). Within foraging dives more prey capture attempts occurred in sinuous $phases_{BS}$ ($hunting_{BS}$). This is in accordance with Plötz *et al.* (2001) who showed that intensification of jaw movements during the bottom $phase_{CA}$ of Weddell seal dives were associated with wiggles. Several studies of free-ranging penguins using time-depth data have confirmed that vertical sinuosity was correlated to the occurrence of feeding events measured independently with changes in oesophageal temperature, beak opening events and integrated acceleration-

video records (Simeone & Wilson 2003; Bost *et al.* 2007; Hanuise *et al.* 2010; Watanabe & Takahashi 2013a). In pinnipeds, vertical sinuosity has also been related to prey capture based on drops in stomach temperature (Horsburgh *et al.* 2008). Furthermore, (Fuiman *et al.* 2007) used video and data recorder to study the 3D dive profiles of Weddell seals in relation to prey encounter and confirmed that vertical sinuosity in time-depth profiles actually occurs during prey encounter.

5.2 Fine scale foraging strategy of Weddell and southern elephant seal

While we are unable to make formal statistical comparisons between the two species due to our sample size, qualitatively we noticed two principal behavioural differences between the SES and Weddell seal: (i) transit $phases_{BS}$ were shorter than hunting $phases_{BS}$ for the Weddell seal whereas they were longer for SES; (ii) hunting $phases_{BS}$ mostly occurred above the bottom $phase_{CA}$ for the Weddell seal whereas they occurred mostly in the bottom $phase_{CA}$ for the SES. These differences probably reflect different foraging strategies between the two species.

Similarly to previous studies, the two SES females essentially used the Antarctic shelf break at sea-ice margin whereas the Weddell seal essentially dived in the fast-iced shallow coastal area in front of Dumont D'Urville (Bailleul *et al.* 2007; Heerah *et al.* 2012). SES performed deeper dives than the Weddell seal and must allocate more time travelling to and from the surface, therefore decreasing the time spent in hunting $mode_{BS}$. Previous studies of Weddell seals using animal borne video and data recorder have shown that the bottom $phase_{CA}$ of dives was associated with significantly higher prey availability than the descent and ascent $phase_{CA}$ (Watanabe *et al.* 2003; Mitani *et al.* 2004). Even though we

found that hunting mode$_{BS}$ also occurred during the bottom phase$_{BS}$, it mostly occurred at shallower depths for the Weddell seal. Weddell seals are opportunistic predators feeding both on pelagic prey such as *Pleuragramma antarcticum* and squid, and benthic prey such as *Trematomus* fish species and invertebrates (Green & Burton 1987; Castellini *et al.* 1992b; Burns *et al.* 1998). Their opportunistic behaviour has also been observed during summer where the three dimensional use of the space under the ice by the Weddell seals suggested that they were searching for prey throughout their dive instead of targeting one depth (Hindell *et al.* 2002).

In contrast, even though we found SES mostly intensified their foraging activity at the bottom of their dive, 43 % of their hunting phases$_{BS}$ still occurred above the bottom phase$_{CA}$. This could be related to a more consistent pattern in their foraging strategy due to a more specialized diet. Indeed, SES females essentially perform pelagic dives and a recent study has shown that they were mostly feeding on myctophid fishes (Hindell *et al.* 1991; Cherel *et al.* 2008). However, our results suggest that considering only the bottom phase$_{CA}$ to fully describe a SES's foraging strategy is probably misleading.

For both species the foraging behaviour revealed by the broken stick was complex. Dives contained on average six or seven behavioural phases$_{BS}$ instead of just three, and hunting mode$_{BS}$ was exhibited on average two and three times a dive, for the Weddell seal and the SES, respectively. Bottom time$_{CA}$ was also significantly higher and lower than hunting time$_{BS}$ for SES and the Weddell seal, respectively, giving a different estimation of the time spent foraging when compared to the time spent hunting$_{BS}$. It is therefore likely that instead of targeting only one type of prey at a particular depth, SES and Weddell seals may also change behaviour mid-dive, to accommodate the sudden appearance of prey. Our novel method allows a more accurate description of the within dive foraging behaviour than when using the bottom time$_{CA}$ only.

6. Conclusion

Our study emphasizes the complexity of SES and Weddell seals diving behaviour, suggesting that using bottom $time_{CA}$ only as an index of intensive foraging may lead to an inaccurate estimation of their foraging activity. Our results also suggest that the Weddell seal is an opportunistic feeder capable of chasing prey in different parts of the water column during a single dive whereas the SES mostly increased their foraging effort during the bottom part of their dives. The integration of instrumentation such as video recorders or stomach/oesophageal temperature sensors, from which prey capture success could be inferred, would help validate the method further (Bost *et al.* 2007; Horsburgh *et al.* 2008; Davis *et al.* 2012; Watanabe & Takahashi 2013a). This study was based on three individuals of two species but it relies on a broken stick method which detects changes in a dive profile and metrics that can be easily implemented in all diving animals. The consistency observed in foraging strategies across different species (Schreer *et al.* 2001) suggests that this method could be applied to other species and would be a useful tool to detect behavioural changes when only time-depth data of a sufficient resolution are available.

7. Acknowledgements

We are grateful to V. Andrews-Goff, S. Blanc, A. Jacquet-Chaboisson, E. Antoine and all volunteers from the 56th, 57th and 58th scientific missions at Dumont d'Urville who assisted in the field. We thank the Institut Polaire Français Paul Emile Victor (IPEV programs 109 and 394), Terres Australes et Antarctiques Françaises (TAAF) and the Australian Antarctic Division for providing logistical support. We wish to thank F. Roquet for his help on the computation of the broken stick algorithm, A.C. Dragon, Y. Ropert-Coudert, C.-A. Bost, and J. Vaquié-Garcia for their advices and support.

8. Appendix

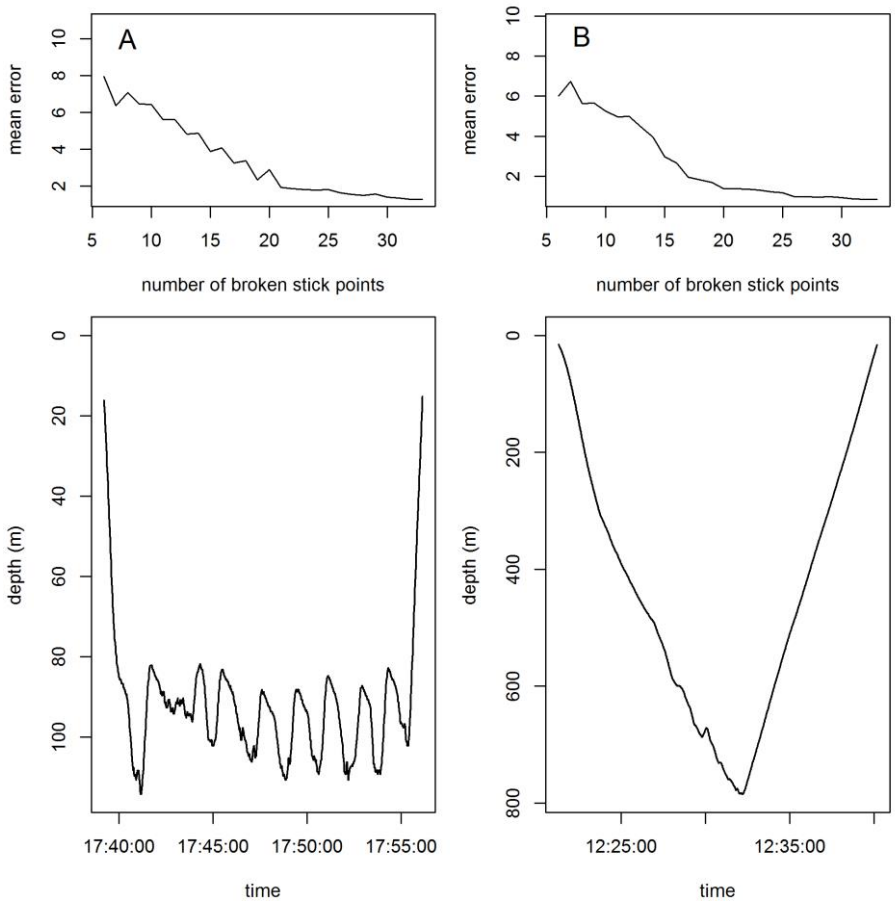

Figure S2.1. Examples of dives for which the Gompertz model did not work. Upper graph: Mean distance according to the number of broken stick points (from 6 to 33) that could be used to describe the dive represented below. The mean distance is the average of the differences between each data point of the original profile and the corresponding point of the reconstructed profile obtained by linear interpolation between the broken stick points (from 6 to 33). Lower graph: original dive profile. Graphs A and B are two examples of SES dive types for which the Gompertz model did not work. For these dives, the relationship between the mean distance and the number of broken stick points was more linear. Consequently, the model could not detect an inflexion point

Script S2.1. Algorithm of the automated and optimised broken stick method.

R script that allow to apply the broken stick method on high-resolution dives: (i) selection of the optimal number of broken stick points to summarize the dive, (ii) calculation for each broken stick segment of the vertical sinuosity index, descent/ascent rates, duration and depth associated with and (iii) determination of the behavioural mode$_{BS}$ (hunting vs transit)

according to the 0.9 vertical sinuosity threshold (see Methods and Fig.2.4). **See Appendix B of the thesis.**

Dataset S2.1. Training dataset to run the automated and optimised broken stick algorithm. Dataset of 1000 dives randomly selected from the Weddell seal dives. Depth was sampled every second by the TDRs during six winter months in 2008 in the Dumont D'Urville coastal area. **See online version of the paper: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0099329**

C - Paper 3

Under revisions in *Animal Biotelemetry* - Proceedings of the bio-logging V

From high-resolution to low-resolution dive datasets: a new index to quantify the foraging effort of marine predators.

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1. Abstract

In the last decade thousands of Satellite Relayed data Loggers (SRDLs) have been deployed, providing large datasets on marine predator movement patterns and their diving behaviour. However, the latter is in a highly summarised form, from which it is difficult to make the sorts of important behavioural inferences that are possible from higher resolution data sets (such as detection of likely foraging events). The main objective of this study was to develop a simple but accurate tool to detect and quantify within-dive foraging periods in low resolution dives. Two southern elephant seals were fitted with a head mounted TDR (recording depth at 1 Hz) and an accelerometer (recording 3 axes of acceleration at 16 Hz) from which prey capture attempts were estimated (PrCA). A Weddell seal was also fitted with a simple TDR (1 Hz).The resulting high-resolution dive profiles were used to: (i) calculate an accurate index of foraging effort based on the detection of vertical sinuosity switches (*i.e.* $\text{hunting}_{\text{highres}}$ time), (ii) produce a SRDL equivalent low-resolution dataset using a broken stick algorithm, (iii) then, a set of candidate foraging effort indices were calculated for each low-resolution dive. $\text{Hunting}_{\text{lowres}}$ time, which is the total time spent in decreased vertical velocity segments of the dive, was the best correlated with $\text{hunting}_{\text{highres}}$ time. 77% of PrCA in SES occurred in $\text{hunting}_{\text{highres}}$ mode (highly sinuous parts of high-resolution dives) and 71% of those PrCA in SES were also detected using the $\text{hunting}_{\text{lowres}}$ segments. The latter were also associated with four times more PrCA than $\text{transit}_{\text{lowres}}$ segments. We found a low-resolution index which indicates within-dive foraging activity and which identified most PrCA, despite degraded information transmitted by SLDRs. Used in combination with other measurements of the *in situ* environment, the $\text{hunting}_{\text{lowres}}$ index could be used in numerous integrated marine ecology studies, such as habitat use studies that are crucial to facilitate more effective conservation.

Keywords: pinnipeds, argos tags, foraging behaviour, marine ecology, method, accelerometers.

2. Introduction

In natural systems, predators perceive and react to environmental heterogeneity in ways that maximise resource acquisition (MacArthur & Pianka 1966). These reactions are manifested through changes in their movement characteristics (*e.g.* direction, speed, sinuosity) that are likely to reflect the presence, or availability, of prey in the three dimensions of the environment (Fauchald & Erikstad 2002). Determining important habitats and quantifying how physical and biological parameters may influence top predators' behaviour is critical to understanding how a changing environment may influence individuals and populations (Evans *et al.* 2012). For many marine predators, prey capture occurs at depth and deciphering their diving behaviour to understand their foraging strategies has been a challenging issue since the late 1960's (Kooyman 1965).

Bio-logging devices have been fundamental in understanding the behaviour of an increasing number of marine species because they allow remote measurements of movements and diving behaviour of free-ranging species (Evans *et al.* 2012). During the last decade Satellite Relayed Data Loggers (SRDLs) have been widely used for transmitting, in near real time, data on the behaviour of marine predators, most typically dive depth and duration, but also in some cases swimming speed or ocean data such as temperature and salinity (Block *et al.* 2011; Fedak 2013).The miniaturisation, extended battery life and memory size allow the collection and storage of data at very high-resolutions (one second or less) and for long periods of time (several months) (Evans *et al.* 2012). However, the limited time and bandwidth available for data transmission at the surface, imposed by the animal's diving habits and CLS Argos, restrict the amount of data that can be sent (Fedak *et al.* 2002). For example, a SRDLs dive profile that was collected and recorded at 1 Hz might be summarised before transmission to only six points,

representing the main inflection points of the full profile, providing less detailed information on the actual dive profile (Fedak *et al.* 2001).

Accurate enumeration of feeding events is difficult to obtain for marine predators and so most studies rely on proxies, such as: maximum dive depth, dive duration, bottom time, descent/ascent rates and index of dive shape (Hindell *et al.* 1991). In marine predators, foraging and prey acquisition are assumed to occur during the bottom phase of the dive, with predators maximising their time at depth (*i.e.* bottom time) and minimising the transit time (*i.e.* descent and ascent phases) (Houston & Carbone 1992). For several species, the duration of the bottom phase has been positively related to foraging activity (Watanabe *et al.* 2003; Austin *et al.* 2006). However, Dragon *et al.* (2012a) and Thums *et al.* (2013) demonstrated that deep foraging dives in southern elephant seals (SES) were associated with high descent/ascent rates but relatively short bottom times. Moreover, a recent study on Weddell and southern elephant seals (SES) demonstrated the three phases model (descent, bottom and ascent) of diving behaviour is overly simplistic and that using the bottom time only as an index of foraging effort can be misleading and inaccurate, because: (i) intensification of the foraging effort could occur several times within a dive and (ii) this may not occur during the bottom phase (Heerah *et al.* 2014).

We studied two deep diving species of circum-Antarctic seals for which, numerous large low-resolution datasets (*i.e.* via SRDLs) are available. Southern elephant seals are capable of travelling long distances from their sub-Antarctic breeding colonies and using diverse habitats (Biuw *et al.* 2007), feeding mainly on fish and squid but also on krill (Cherel *et al.* 2008; Walters *et al.* 2014). Their diving behaviour is relatively stereotyped and they mostly forage at the bottom of their dives (Guinet *et al.* 2014). In contrast, Weddell seals mainly reside in coastal waters in fast-iced areas. They feed mainly on fish, but also on cephalopods and crustaceans according to age, location and season (Lake *et al.* 2003).

Their diving behaviour seems to reflect this generalist feeding strategy even at the scale of the dive, with seals foraging several times within a dive, mostly above the bottom phase of the dive (Heerah *et al.* 2014). Southern elephant and Weddell seal foraging behaviour has been extensively studied in several locations (Plötz *et al.* 2001; Naito *et al.* 2010; Dragon *et al.* 2010; McIntyre *et al.* 2011). However, the new information on fine-scale behaviour by (Dragon *et al.* 2012a) and (Heerah *et al.* 2014) in addition to the increasingly large number of low-resolution data available highlight the value of re-visiting the common approach of identifying foraging activity within low-resolution dives.

We used high resolution Time Depth Recorder (TDR) and acceleration datasets from two SES during their post-breeding foraging trip, and a high-resolution TDR dataset from a Weddell seal during six winter months. These high resolution dive data were degraded into equivalent SRDL low-resolution dives to develop a simple but accurate tool to: (i) detect and quantify within-dive foraging periods, in low dives resolution when no concurrent information on prey encounters are available and (ii) use concurrent prey capture attempts (PrCA) estimated for the SES from high-resolution acceleration data to independently validate the most promising low-resolution index.

3. Material and Methods

Two adult female SES (length: 266 and 255 cm) were captured at Kerguelen Island (49°20’ S, 70°20’ E) in early November 2010 before their post-breeding foraging trip. One adult female Weddell seal was captured in February 2008 after its annual moult at Dumont D’Urville (66°40’ S, 140°00 E) (length 230 cm). Similar capture and tagging procedures were used for both species and are fully described in (Heerah *et al.* 2014). A TDR combined with an accelerometer (TDR Mk 10 X, Wildlife Computers) and a TDR (Mk 10, Wildlife Computers) was head-glued to the SES and to the back of the Weddell seal, respectively. The TDRs all recorded depth at 1Hz. For the SES, acceleration was recorded in all 3 axes at 16 Hz.

The number of prey capture attempts (PrCA) were calculated for each dive from the concurrent high-resolution acceleration data. A full description of the acceleration data filtration process and definition of PrCA occurrence are given in (Guinet *et al.* 2014).

3.1 Fine scale analysis of foraging behaviour

The high-resolution dive data were processed with a new approach which accurately identifies the parts within a dive where a diving predator displays foraging behaviour based on the vertical sinuosity in the dive profile (Heerah *et al.* 2014). Only dives below 20 meters were analysed for both species. The method is fully described in (Heerah *et al.* 2014) and briefly summarized below. Each dive was summarised by an optimised broken stick algorithm which: (i) iteratively selected a series of inflexion points for individual dives. Multiple summaries were made for each dive based on a varying number of inflections, (ii) selected from this suite of summaries, the number of broken stick points (inflections) that

best summarised the dive shape, (iii) subsequently described the complete set of dives independently of their depth, duration and complexity and (iv) calculated for each dive parts (*i.e.* between two inflexion points) an index of vertical sinuosity as the ratio between, (1) the depth difference between the two inflexion points delimiting the dive part considered and, (2) the sum of all the vertical distances the seal has actually swum within that dive part. Vertical sinuosity ratio takes a value of 1 when the individual swims in a straight path during this part of the dive. Any deviation from a straight path decreases the sinuosity ratio toward 0. By expanding the definition of an area restricted search (ARS) from the horizontal dimension into the vertical dimension, the approach detects two types of behaviour according to their sinuosity, with: (i) highly sinuous segments indicating "hunting" ($0 <$ vertical sinuosity > 0.9) and (ii) less sinuous segments indicating "transiting" ($0.9 \leq$ vertical sinuosity ≥ 1). The time spent in hunting mode within a dive was summed for each dive and used as an index of the foraging effort (hereafter, "$\text{hunting}_{\text{highres}}$ time"). Dives with more than 1500 seconds spent in $\text{hunting}_{\text{highres}}$ time were scarce and therefore not considered in further analysis (9 and 10 dives for the SES and the Weddell seal, respectively).

As described in (Heerah *et al.* 2014), dives of the Weddell seal dataset containing segments associated with abnormally high vertical ascent/descent rates were removed (23 dives in the Weddell seal dataset).

3.2 From high-resolution to low-resolution dive datasets

3.2.1 Simulation of a low-resolution dive dataset and calculation of foraging effort indices

In order to quantify the foraging effort in low-resolution dives it was necessary to find an index similar to the $hunting_{highres}$ time. First, we used the high-resolution dives to generate the equivalent low-resolution profiles provided by CTD-SRDLs (Conductivity Temperature Depth-Satellite Relayed Data Loggers) using a broken stick algorithm (Fedak *et al.* 2001). The SRDL datasets were created by selecting six data points for each high-resolution dive: the two surface points marking the beginning and end of each dive, the maximum depth point and the three other most informative inflexion points. This is the same method used to summarise dive data transmitted by SRDLs (Fedak *et al.* 2001).

Then for each dive we calculated five different indices that could be potentially used to infer foraging effort:

1. The time spent at more than 80, 65 and 60% of the maximum dive depth (hereafter, bt80, bt65 and bt60). Foraging is often assumed to occur during the bottom phase of a dive with bt80 being used as an index of foraging effort for low-resolution dives (Burns *et al.* 2008; Heerah *et al.* 2012). However, foraging activity also occurs above the bottom phase (Watanabe *et al.* 2003). We therefore calculated the bt65 and bt60 in order to encompass a broader range of within-dive activity.
2. The rate of change ($m.sec^{-1}$) between the surface and the first inflexion point (*i.e.* descent rate). The broken stick algorithm detects the most informative changes in a dive profile, therefore this first part of the dive is the most likely to reflect the dive descent.
3. The rate between the last broken stick inflexion point and surface (*i.e.* ascent rate).

For the same reason as explained above, the last broken stick inflexion point was used to define the beginning of the dive ascent.

We tested descent and ascent rates as possible candidates of foraging effort indices as they can reflect prey patches that a seal would want to reach and return to faster (Thums *et al.* 2013) but also impact the time allocated to foraging activity due to its energetic costs (Williams 2000).

4. Time allocation at depth index (TAD) (Fedak *et al.* 2001). The index takes values close to 1 when the area enclosed by the dive profile is maximal (i.e. "square-shaped dive") toward values close to 0.5 when the dive area is minimum (i.e. "V-shaped dive") given a set speed. The V-shaped dive represents dives where equal time is spent at all the depths encountered. Conversely, the square-shaped dive represents dives where a seal maximises its time at a given depth, reflecting potential foraging activity.
5. Hunting time calculated using low-resolution dive data (i.e. $hunting_{lowres}$ time). A recent study has shown that hunting mode in high-resolution dives (calculated using vertical sinuosity, see (Heerah *et al.* 2014), Fig. 3.1a, c) was associated both with more PrCA and decreased vertical velocities (SES: 0.3 ± 0.001 m.sec $^{-1}$, Weddell seal: 0.13 ± 0.13 m.sec $^{-1}$; (Heerah *et al.* 2014). However, vertical sinuosity cannot be calculated for low-resolution dives. Instead, for each low-resolution dive broken stick segment we calculated the concurrent vertical rate of change (m.sec $^{-1}$, Fig. 3.1b, d, Fig. 3.2). According to the results from high-resolution dives and the

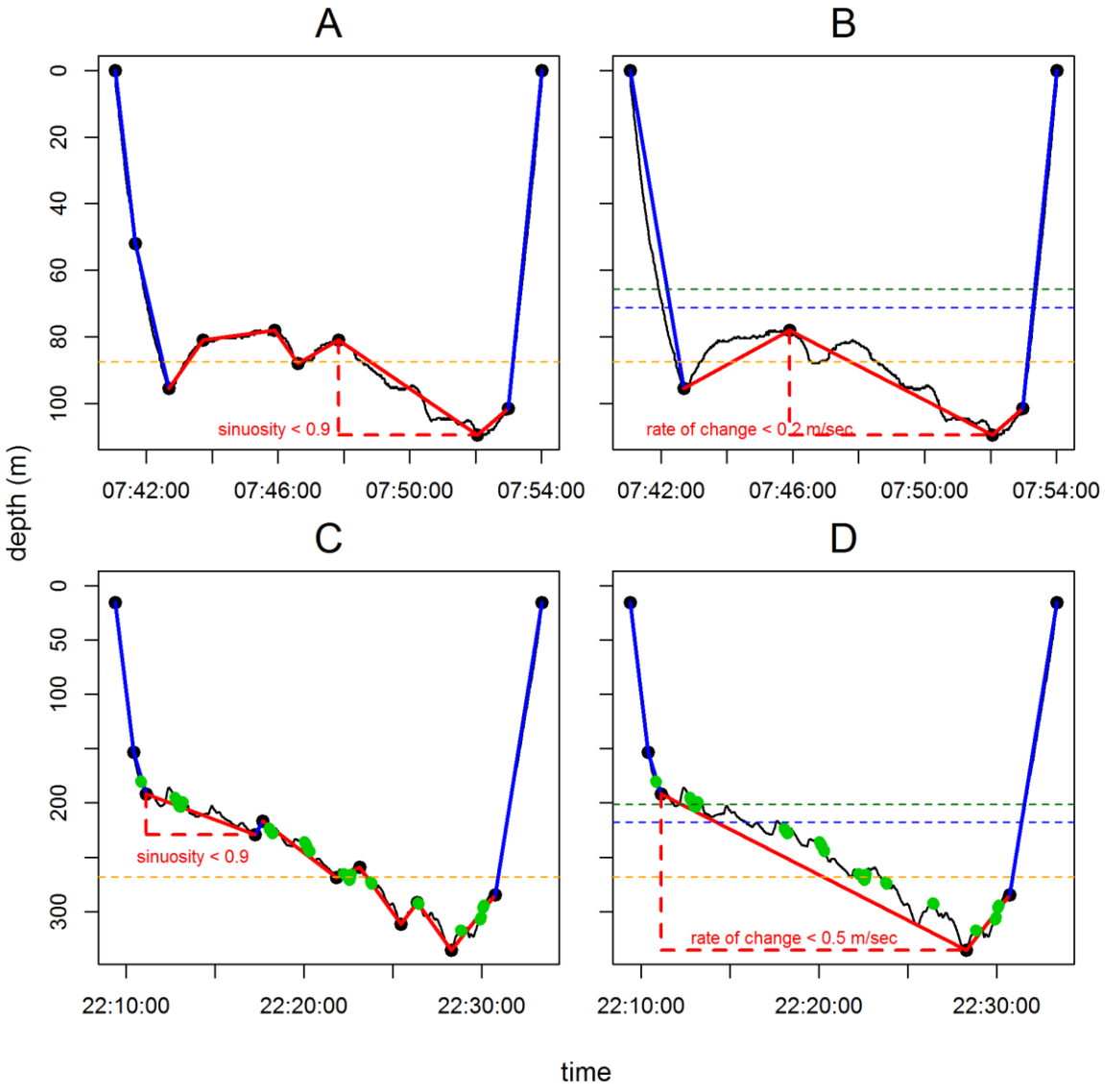


Figure 3.1. From high-resolution to low-resolution dive profiles: detection of intensive foraging. High-resolution dive profile (black line) were summarised by the optimal broken stick method (A: Weddell seal, C: SES) and degraded in SRDLs low-resolution dives (B: Weddell, D: SES). Red lines represent broken stick segments associated with the "hunting$_{highres}$" (*i.e.* highly sinuous parts of high-resolution dives) and "hunting$_{lowres}$" (*i.e.* segments associated with a reduced vertical velocity in low-resolution dives, see Fig.3.2) modes. Conversely, blue lines represent broken stick segments associated with the "transit$_{highres}$" (*i.e.* straighter parts of high-resolution dives) and "transit$_{lowres}$" (*i.e.* segments associated with an increased vertical in low-resolution dives, see Fig.3.2) modes. Dotted lines represent the 80 (orange), 65 (blue), 60 (green) % of maximal dive depth. The green dots indicate PrCA for SES dataset (estimated from high-resolution acceleration data).

distribution of vertical velocity in low-resolution dives, we used thresholds of: (i) 0.2 m.sec $^{-1}$ for the Weddell seal (Fig. 3.2a) and (ii) 0.5 m.sec $^{-1}$ for the SES (Fig. 3.2b) to discriminate between "low speed" (hereafter "hunting$_{lowres}$") segments vs "high speed" (hereafter "transit$_{lowres}$") segments in low-resolution dive data (Fig. 3.1c, d). The total time spent in "hunting$_{lowres}$" segments for each dive was used as a candidate index of foraging effort (*i.e.* within-dive hunting time for low-resolution dive data – hereafter "hunting$_{lowres}$ time").

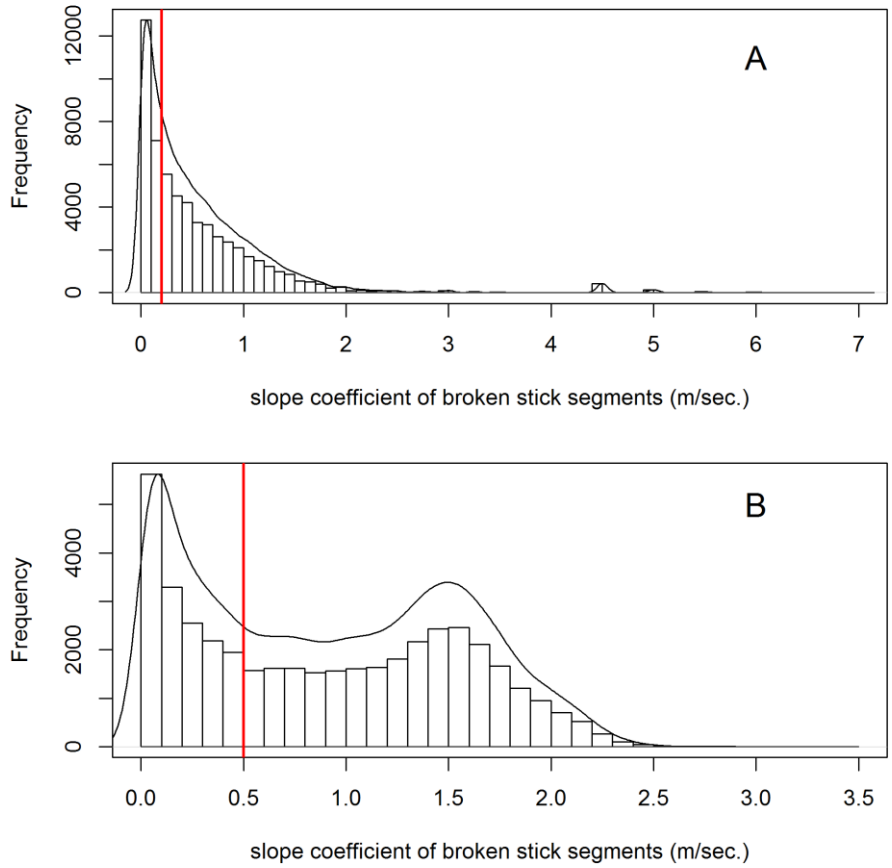


Figure 3.2. Distribution vertical velocity in low-resolution dives. Distribution of the vertical velocity (histogram and density plot [black line]) associated to each broken stick segment in low-resolution dives for the Weddell seal (A) and the SES (B). The treshold of 0.2 m.sec -1 for the Weddell seal (A) and 0.5 m.sec -1 for the SES (B) were used to discriminate "low speed" (i.e. "huntinglowres") segments versus "high speed" (i.e. "transitlowres") segments in low-resolution dive data. The total time spent in "huntinglowres" segments for each dive was used as an index of foraging effort (i.e. "huntinglowres time").

3.2.2 Statistical analysis

The relationship between the five low-resolution foraging indices and the $hunting_{highres}$ time was analysed using Spearman correlations (function *cor;* R Development Core Team 2008) and this indicated that $hunting_{lowres}$ time was best correlated with the $hunting_{highres}$ time (R^2 SES = 0.61, R^2 Weddell seal = 0.90, Table 3.S1). We therefore fitted linear models to investigate the relationship between the $hunting_{highres}$ time and the $hunting_{lowres}$ time (function *lm;* R Development Core Team 2008) for both species. The residuals of this preliminary fit showed that some dives were not well explained by the model and weakened the relationship despite only representing 1.4% and 6% of the dataset for the Weddell seal and the SES, respectively (Fig. S3.1). For the SES they were dives associated with: (i) $hunting_{lowres}$ time = 0 and $hunting_{highres}$ time ≥ 300 sec. (*i.e.* underestimation with low-resolution index) and (ii) dives associated with residuals ≤ -300 (*i.e.* overestimation with low resolution index) (see Fig. S3.1). For the Weddell seal they were dives associated with $hunting_{lowres}$ time = 0 and $hunting_{highres}$ time ≥ 150 sec. (i.e. underestimation with low-resolution index) (see Fig. S3.1). These dives were excluded from the dataset before repeating the analysis described above.

4. Results

4.1 General diving behaviour

The TDRs recorded the diving behaviour of two SES for 72 and 73 days from November to January 2011 (Table 3.1). The seals performed 3941 and 4254 dives with on average (mean ± SD) 53 ± 1 and 56 ± 1 dives per day, respectively (Table 3.1). The mean maximum dive depths were 511 ± 4 m and 475 ± 4 m with in average dive durations of 23 ± 0.01 min and 21 ± 0.1 min, and dives were associated with 8 ± 0.06 and 10 ± 0.05 PrCA, respectively (Table 3.1). The diving behaviour of the Weddell seal was recorded for 182 days from February to August 2008 (Table 3.1). The seal performed 11452 dives with on average 63 ± 24 dives per day (Table 3.1). The mean maximum dive depth was 67 ± 54 m with in average dive durations of 10 ± 6 min (Table 3.1).

Table 3.1. Summary of deployment and dive data collected. General tag transmission and diving behaviour data are presented for two adult female southern elephant seals (SES) and one adult female Weddell seal captured at Kerguelen Island and Dumont d'Urville, respectively. Both species were fitted with TDRs and accelerometers were also head-mounted on SES from which prey capture attempts (PrCA) were calculated.

	Tag deployment	Tag retrieval	Transmission duration (days)	Number of dives	Number of dives per day	Dive maximum depth (m)	Dive duration (min)	N PrCA
SES 1	2010-10-31	2011-01-21	72	3941	53 ± 1 max: 68	511 ± 4 max: 1260	23 ± 0.01 max: 56	8 ± 0.06 max : 39
SES 2	2010-01-11	2011-01-15	73	4254	56 ± 1 max: 104	475 ± 4 max: 1296	21 ± 0. 1 max: 50	10 ± 0.05 max : 40
Weddell seal	2003-02-23	2008-10-20	182	11452	63 ± 24 max: 115	67 ± 54 max: 645	10 ± 6 max: 46	NA

4.2 From high-resolution to low-resolution dives: estimation of foraging effort

4.2.1 Comparison between foraging effort metrics

Of all the low-resolution dive foraging effort indices, the $hunting_{lowres}$ time (see method section 2.2.1) was best correlated with the $hunting_{highres}$ time for both species (R^2 SES = 0.74 and R^2 Weddell seal = 0.91, Table 3.2). Two dives for each species are presented as an example of the concordance between the parts of the dive where foraging occurred for high and low-resolution dives, respectively (Fig. 3.1).

Table 3.2. Correlations between high and low-resolution foraging effort indices. R^2 of Spearman correlations between high-resolution and low-resolution foraging effort indices after removing dives associated with outlier residuals (see material and methods section 2.2.2 and Table S3.1). $Hunting_{highres}$ time is the total time spent in "$hunting_{highres}$" mode (see Fig..3.1 for description) per high-resolution dive. The low-resolution dive foraging effort indices are: the time spent below 80, 65 and 60% of the maximum dive depth (bt80, bt60 and bt65), the descent/ascent rate from/to the surface to/from the first/last broken stick inflexion point, the time allocation at depth index (TAD index) and the $hunting_{lowres}$ time (see Fig.3.1 and 3.2 for description).

Low-resolution dive foraging effort indices	**$Hunting_{highres}$ time**	
	Weddell seal	SES
Bt60	0.72	0.38
Bt65	0.67	0.41
Bt80	0.50	0.32
Desc_rate	-0.16	-0.003
Asc_rate	-0.20	0.0006
TAD index	0.03	0.17
$Hunting_{lowres}$ time	**0.91**	**0.74**

For the SES, the second best correlated index with $hunting_{highres}$ time was bt65 followed by bt60 and bt80 ranging from an R^2 value of 0.3 to 0.4. The ascent rate correlated least with $hunting_{highres}$ time (R^2 = -0.0006, Table 3.2). For the Weddell seal, the second

best correlated index with $hunting_{highres}$ time was bt60, followed by bt65 and bt80 ranging from an R^2 value of 0.5 to 0.7 (Table 3.2). The TAD index correlated least with $hunting_{highres}$ time ($R^2 = 0.03$, Table 3.2).

4.2.2 Relationship between low and high-resolution dive index of foraging effort

Linear models were fitted to $hunting_{highres}$ time and $hunting_{lowres}$ time for each species. Dives associated with outlier residuals were removed from our dataset (see methods section 3.2.2 and Fig. S3.1). Models were then fitted on the remaining 7703 and 11227 dives for SES and the Weddell seal, respectively. Removing a small percentage of outlier dives (6 and 1.4 % of the dataset for SES and the Weddell seal, respectively) improved the fit of the model (see distribution of the residuals Fig. S3.2 [before] and 3 [after]) and the strength of the relationship between the variables for both species, particularly for SES (Fig. S3.2 [before] and Fig. 3.3 [after]). The relationship between $hunting_{highres}$ time and $hunting_{lowres}$ time was positively significant (p-value < 0.001) for both species, but stronger for the Weddell seal (R^2 SES = 0.74 and R^2 Weddell seal = 0.91, Fig. 3.3, Table 3.2).

On average, $hunting_{highres}$ time was 9 ± 0.05 min and 6.5 ± 0.05 min per dive representing 42 ± 0.2 % and 59 ± 0.3 % of the corresponding dive duration, for SES and the Weddell seal, respectively (see Heerah *et al.* 2014). On average, $hunting_{lowres}$ time was 10 ± 0.06 and 6 ± 0.05 min per dive representing 48 ± 0.3 % and 54 ± 0.3 % of the corresponding dive duration, for SES and the Weddell seal, respectively. Southern elephant seals spent 41 and 47% of their total dive duration foraging when considering $hunting_{highres}$

and hunting$_{lowres}$ time, respectively. The Weddell seal spent 67 and 62% of their total dive duration foraging when considering hunting$_{highres}$ and hunting$_{lowres}$ time, respectively.

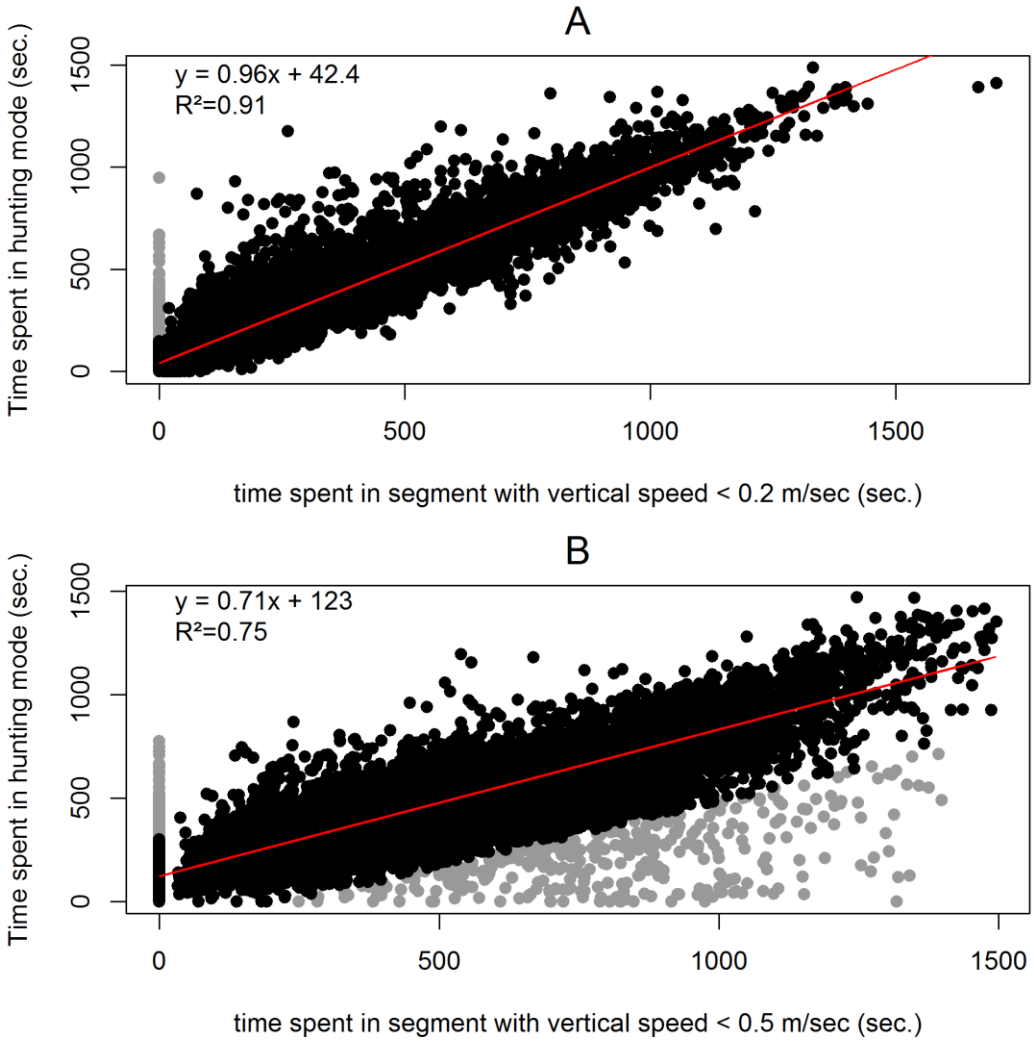


Figure 3.3. Relationship between high-resolution and low-resolution foraging effort metric. Results of linear models fitted to investigate the relationship between the huntinghighres time (see Table 3.2 and Fig.3.1 for description) and the huntinglowres time (see Fig.3.1 and 3.2 for description) for the Weddell seal (A) and the SES (B). The regression line of the model is represented in red. Grey points indicate dives associated with outlier residuals that were removed: 6 and 1.4% of the SES and Weddell seal dataset, respectively (see material and methods section 2.2.2 and Fig. S3.2).

4.2.3 Foraging effort and prey capture attemps in SES

In SES high-resolution dives, $hunting_{highres}$ phases (*i.e.* successive segments of same behavioural mode) were associated with four times more PrCA than $transit_{highres}$ phases (Table 3.3) with 77 % of the PrCA occurring during hunting phases (Fig. 3.1c, see Heerah *et al.* 2014). In SES low-resolution dives, $hunting_{lowres}$ segments were also associated with four times more PrCA (Table 3.3) than $transit_{lowres}$ segments with 71 % of the PrCA occurring within low speed segments (Fig. 3.1d).

Table 3.3. Prey encounter occurrences. Number of prey capture attempts (PrCA) in SES dives according to the foraging behaviour. $Hunting_{highres}$ and $hunting_{lowres}$ phases (see Fig.3.1 for description) indicate parts within a high and low resolution dive, respectively, where a seal intensifies its foraging behaviour.

		Intensified foraging effort	**Transit**
N PrCA	High resolution	2.5 ± 0.02	0.6 ± 0.007
	Low resolution	4 ± 0.04	1 ± 0.01
% of total PrCA	High resolution	77	23
	Low resolution	71	29

5. Discussion

We present a new method for identifying areas of hunting activity within low-resolution dive data, which can be used at the scale of individual dives. Our results show that (i) of five potential indices, the $hunting_{lowres}$ time was the most correlated of the indices to the $hunting_{highres}$ time, (ii) times allocated to foraging at the dive or trip scale were similar when estimated by $hunting_{highres}$ and $hunting_{lowres}$ time, (iii) 77% of the PrCA occurred in $hunting_{highres}$ mode segments of high-resolution dives and despite dive information being much more degraded in low-resolution dives, 71 % of the PrCA occurred in the $hunting_{lowres}$ segments which were also associated with four times more PrCA than $transit_{lowres}$ segments. Importantly, the concurrent prey capture attempts (PrCA) estimated from high-resolution acceleration data for SES supported the low-resolution foraging effort index identified with our method.

Unlike studies that only consider foraging behaviour within the bottom phase of a dive (Dragon *et al.* 2012a), the "hunting time" method (Heerah *et al.* 2014) encapsulates all foraging activity within a dive. We show that the same method can be applied to low-resolution dive data from SRDLs and this method still detects foraging within a dive and most of the associated PrCA, despite being highly degraded information.

5.1 Foraging effort in low-resolution dives

5.1.1 $Hunting_{lowres}$ time

Of all the low-resolution foraging effort indices tested, the $hunting_{lowres}$ time was the best correlated to the $hunting_{highres}$ time. The strong correlation between $hunting_{highres}$ and $hunting_{lowres}$ time indicates that low-resolution dive segments of decreased vertical

velocity (*i.e.* "hunting$_{lowres}$ mode") are also associated with increased vertical sinuosity (*i.e.* wiggles). Vertical sinuosity is a feature captured by high-resolution dive data, often used as an index of foraging effort and/or feeding success, even when no independent information on prey capture is available (Hindell *et al.* 1991).

Similar to the hunting$_{highres}$ time, the hunting$_{lowres}$ time has the advantage of incorporating the entire dive profile to detect intensified foraging effort according to behavioural changes (see Heerah *et al.* 2014) rather than a putative bottom phase. Acceleration data cannot discriminate between successful PrCA and unsuccessful ones and may not represent actual feeding success, although it is a powerful proxy for quantifying predator-prey encounters (Watanabe & Takahashi 2013a) providing valuable information on the distribution and abundance of prey in the water column (Naito *et al.* 2013). The results are concordant with our assumption that diving predators adjust their diving behaviour to maximise the time spent in a prey patch by displaying vertical ARS (*i.e.* increased vertical sinuosity and decreased vertical speed). Consequently, hunting$_{lowres}$ mode segments and hunting$_{lowres}$ time could be used as a tool to: (i) accurately isolate areas of foraging behaviour within a dive and (ii) quantify the overall dive foraging effort using only low-resolution dive datasets.

5.1.2 Bottom time indices

Although not the best indices, bottom times (bt80, bt65 and bt60) were also correlated with hunting$_{highres}$ time for both species. It is a commonly accepted idea that foraging activity mainly occurs during the bottom phase of a dive (Watanabe *et al.* 2003), and so some measure of bottom time is often used as an index of foraging effort to investigate habitat use and dive behaviour (Bailleul *et al.* 2010b). However, using only bt80

as an index of foraging effort in low resolution dives would be misleading in over- (SES) or under-estimating (Weddell seal) the actual time spent in intensive foraging mode (see Heerah *et al.* 2014). Further, hunting occurred several times within a dive, and not always during the bottom phase. For SES, hunting occurred mostly in the bottom phase, but could also occur at shallower depths within a dive. For the Weddell seal, intensive foraging activity predominately occurred above the bottom phase (Heerah *et al.* 2014). This is perhaps why, for Weddell seals, incorporating a greater proportion of the dive profile in the bottom phase to calculate the bt (from bt80 to bt60) strengthened the correlations with $hunting_{highres}$ time. A similar trend was observed for the SES (up to bt65) after which the correlation decreased. Southern elephant seals perform deeper dives than Weddell seals and must therefore allocate more transit time between the surface and dive bottom. For SES it is likely that bt60 includes both foraging and transit activity, thus weakening the correlation with $hunting_{highres}$ time. Consequently, we see two main limitations of using bottom time indices: these methods (1) only consider a proportion of the dive profile and it is often difficult to accurately define the actual bottom phase; and (2) assume that foraging is occurring only in one part of the dive instead of considering behavioural variations within the dive. Alternatively, the "$hunting_{lowres}$ time" method is a more appropriate measure of foraging effort because it incorporates the entire dive profile and detects within-dive behavioural changes.

5.1.3 TAD and transiting rate indices

For both species, there were weak correlations between the TAD index, the descent/ ascent rates and $hunting_{highres}$ time. Dive classification studies often assume that square shaped dives are foraging dives (Schreer *et al.* 2001). However, our results suggest that

attributing an overall function to the dive based only on its shape might oversimplify the complexity of the within-dive activity of diving predators. Indeed, Heerah *et al.* (2014) demonstrated the dive complexity of seals (both Weddell seal and SES) that alternated between transit and hunting behaviour several times within each dive. We tested descent and ascent rates as possible candidates of foraging effort indices as both are known to influence foraging activity of marine predators in different ways: (i) reflect favourable areas that a seal would want to reach and return to faster (Thums *et al.* 2013), (ii) be used to prospect the water column and find a patch of prey (Charrassin & Bost 2001) (iii) impact the time allocated to foraging activity due to its energetic costs (Williams 2000). Without any information on changes in body condition or metabolic rate it is difficult to draw conclusions based on these assumptions. However, our results suggest that only using transit rates poorly reflects the time spent in intensive foraging.

5.2 Ecological applications

During the last decade SRDLs have been widely deployed on several species. These tags were primarily designed to monitor animal behaviour, but the integration of other sensors (temperature, conductivity, ambient light *etc*.) provides insight into the direct responses of individuals to their environment (O'Toole *et al.* 2014). Since 2004, more than 270 000 CTD profiles were collected using CTD-SRDLs from SMRU (Sea Mammal Research Unit, Scotland) in the frame of SEaOS (Southern Elephant Seals as Oceanographic Samplers) and MEOP (**Marine Mammal Exploration of the Oceans Pole to Pole; hooded, crabeater, Weddell and southern elephant seals)** programs (Roquet *et al.* 2013). On average, two CTD profiles per day are transmitted and depending on the species the number of low-resolution dive profiles associated per day can be up to 15 more

times (SES, S. Labrousse unpublished data). Other projects like the Tagging of Pacific Pelagics (TOPP) has also deployed thousands of similar tags including SRDLs (Block *et al.* 2011). These numbers are impressive and show that millions of low-resolution dive profiles were or are to be analysed.

In this study, the $hunting_{lowres}$ time encapsulates similar information to the high-resolution one (*e.g.* detection of behavioural changes, similar proportions of PrCA occurring in intensive foraging mode, quantification of the time spent in hunting mode). We acknowledge that our study was based on three individuals, but it is compensated to some extent by the very large number of high and low-resolution dives included in the analysis.

The behavioural adjustments of top predators when diving are expected to primarily reflect changes in their prey distribution in the three dimensions of the environment (Fauchald & Erikstad 2002). Several methods have been developed to quantify how individuals concentrate their search effort along a given path (*e.g* Hidden Markov model (Patterson *et al.* 2009), first passage time (Fauchald & Tveraa 2003), state space model (Jonsen *et al.* 2005)) and used to relate the defined horizontal ARS to particular structures of the environment (*e.g.* oceanographic features (Muelbert *et al.* 2013), sea-ice (Freitas *et al.* 2009), topography (Andersen *et al.* 2013)). Bailleul *et al.* (2008) underlined the importance of integrating a vertical index of foraging effort to better identify foraging areas when studying deep-diving marine predators. Indeed, for many marine predators, feeding occurs at depth and several studies demonstrated the association between oceanographic features of the water column and predator's diving behaviour (Charrassin & Bost 2001; Heerah *et al.* 2012). The inclusion of $hunting_{lowres}$ time when predicting switching between movement states (see Bestley *et al.* 2012), would allow to integrate a quantification of foraging effort at depth (where they encounter prey) based on the detection of changes in

diving behaviour and to relate actual predator's behaviour in the three dimensions to the heterogeneous environment they respond to.

6. Conclusion

Our study showed that using fundamental but straightforward procedures such as the transposition of the definition of the ARS into the vertical dimension we could find an accurate index that: (i) detects intensive foraging occurrences and (ii) quantify the within-dive foraging effort. Our results also suggested that despite degraded information, insights on foraging activity could be obtained when using low-resolution dive datasets as long as using a metric that is based on the detection of changes in predator's diving behaviour.

Our results were supported by independent PrCA but the integration of complementary sensors (*e.g.* video recorders, stomach/oesophageal temperature sensors) from which feeding success could be inferred would allow to further validate the method (Horsburgh *et al.* 2008; Watanabe & Takahashi 2013a). This method was developed on a small amount of individuals but on two species displaying a broad range of different dive types (Hindell *et al.* 1991; Schreer & Testa 1996). Moreover, the consistency of foraging strategies across different species (Schreer *et al.* 2001) and the simplicity of the index suggest that this method could be applied to a broad range of diving species. For example, the $hunting_{highres}$ and/or $hunting_{lowres}$ time could be included in the metrics calculated on board the tags and provided by SRDLs. This method could be a useful tool in both behavioural and ecological studies to characterize and/or predict at broad and fine scale which environmental features are likely to impact marine predators and their prey.

7. Aknowledgements

This study was supported by an Australian Antarctic Science grant (AAS project 2794), the programs CNES-TOSCA ("Ecologie des phoques de Weddell et bio-océanographie de la banquise antarctique" and "Eléphants de mer océanographes"), the ANR VMC-07: IPSOS seals and the Total foundation. Funding sources had no involvement in the study design, the collection, analysis and interpretation of data. All animals in this study were treated in accordance with the IPEV ethics and polar environment committee guidelines. We thank the IPEV (programs 109 and 394), TAAF and AAD for providing logistical support. We thank all the people that contributed to the field work in Dumont D'Urville and Kerguelen and data processing, especially J. Vaquié-Garcia and V. Andrews-Goff. We wish to thank M. Fedak for his help on the calculation of the TAD index and M. O'Toole for his comments and revisions of the manuscript.

8. Appendix

Table S3.1. R^2 of Spearman correlations between high-resolution and low-resolution foraging effort indices before removing dives associated with outlier residuals (see material and methods section 2.2.2 and Figure S3.1). See Table 3.2 for variable descriptions. SES stands for southern elephant seals.

Low-resolution dive foraging effort indices	**$Hunting_{highres}$ time**	
	Weddell seal	SES
Bt60	0.71	0.38
Bt65	0.67	0.39
Bt80	0.50	0.31
Desc_rate	-0.16	-0.003
Asc_rate	-0.20	0.002
TAD index	0.03	0.18
$Hunting_{lowres}$ time	**0.89**	**0.60**

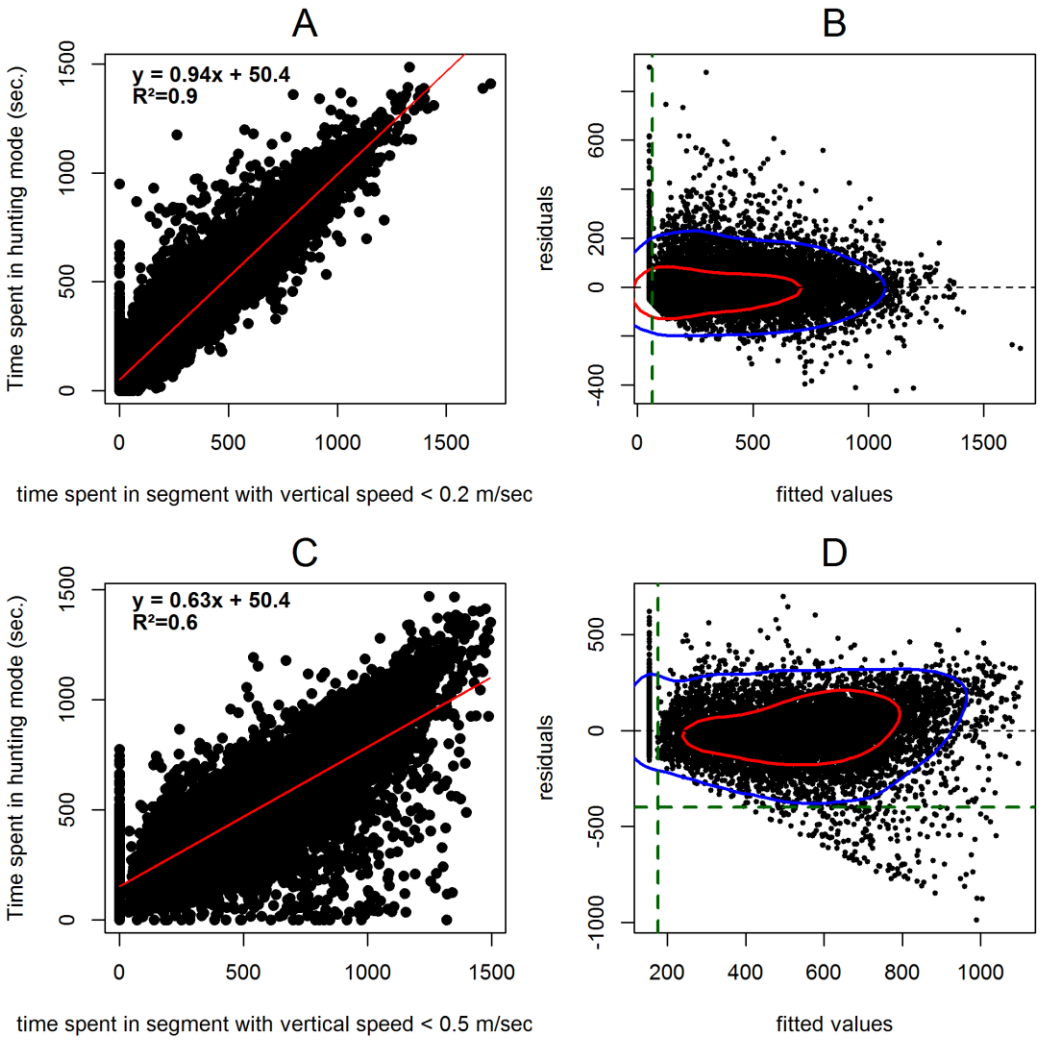


Figure S3.1. Results of the preliminary linear models fitted to $hunting_{highres}$ time (time spent in highly sinuous parts of high-resolution dives) and the $hunting_{lowres}$ time (time spent in segments associated with vertical velocity ≤ 0.2 [Wedell seal] and 0.5 [SES] m.sec $^{-1}$ of low-resolution dive) for the Weddell seal (A) and the SES (C). The regression line of the model is represented in red. Residuals of this preliminary fit are presented for the Weddell seal (C) and the SES (D). Kernel density contour encompassing 90 and 50% of the dives are represented in blue and red, respectively. A small proportion of dives were not well explained by the model: dives on the left and below the green dotted lines and outside of the kernel density contour of 90%.

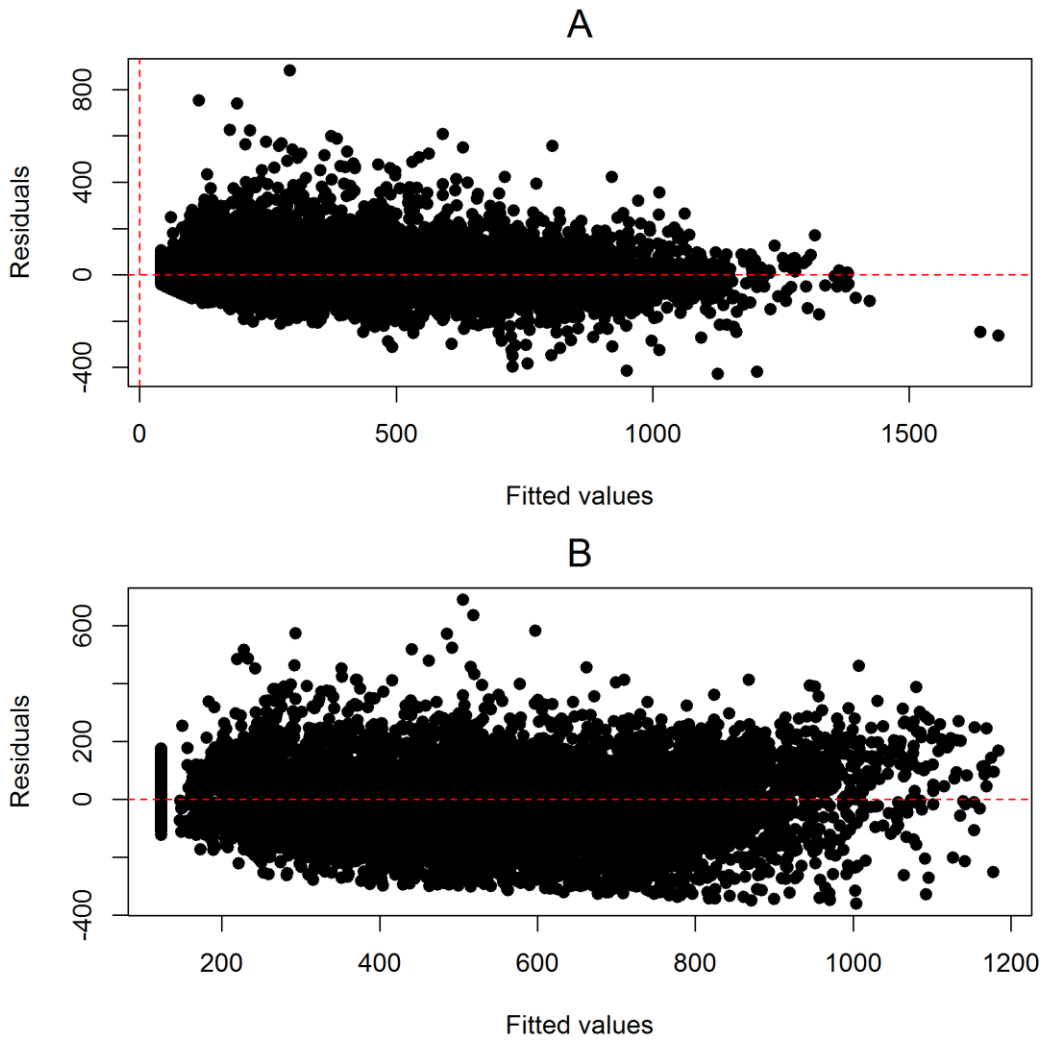


Figure S3.2. Residuals of linear models fitted to $hunting_{highres}$ time and the $hunting_{lowres}$ time for the Weddell seal (A) and the SES (B) after removal of dives associated with outlier residuals (see Figure S3.1).

D - Conclusion

These two chapters showed that using a simple ecological concept of the transposition of horizontal ARS into the vertical dimension, we could accurately: (i) detect intensive foraging behaviour within a dive and (ii) quantify the within-dive foraging effort. We also showed that this approach could be applied both to high and low-resolution dive profiles which is vital considering the number of low-resolution dive profiles available for retrospective and/or future analyses. Moreover, because the foraging metrics used rely on the detection of changes in diving movements, they are easily transposable to any diving species.

The first paper (Paper 2) focused on developing a method to detect foraging activity within high-resolution dives and to validate it using concurrent prey capture attempts for SES. First, high-resolution dives were divided into an optimal number of segments which highlighted the complexity of seal behaviour (for both SES and Weddell seal). The detection of changes in the sinuosity of the seals' diving behaviour allowed identification of the different phases of foraging activity along the whole dive profile, rather than considering the dive bottom phase as the only period of foraging activity. The phases identified by our method as foraging were highly associated with prey capture attempts. This helps validate our approach (vertical ARS assumption) and the sinuosity metric used. SES foraging activity mainly occurred within the bottom phase of the dive (near the maximum depth), whereas Weddell seal foraging activity mainly occurred above the bottom phase. This suggests that the use of bottom time only to calculate a foraging effort index would be inaccurate and/or misleading for some species. This is why we propose the adoption of our method, termed the "hunting method", for identifying foraging activity

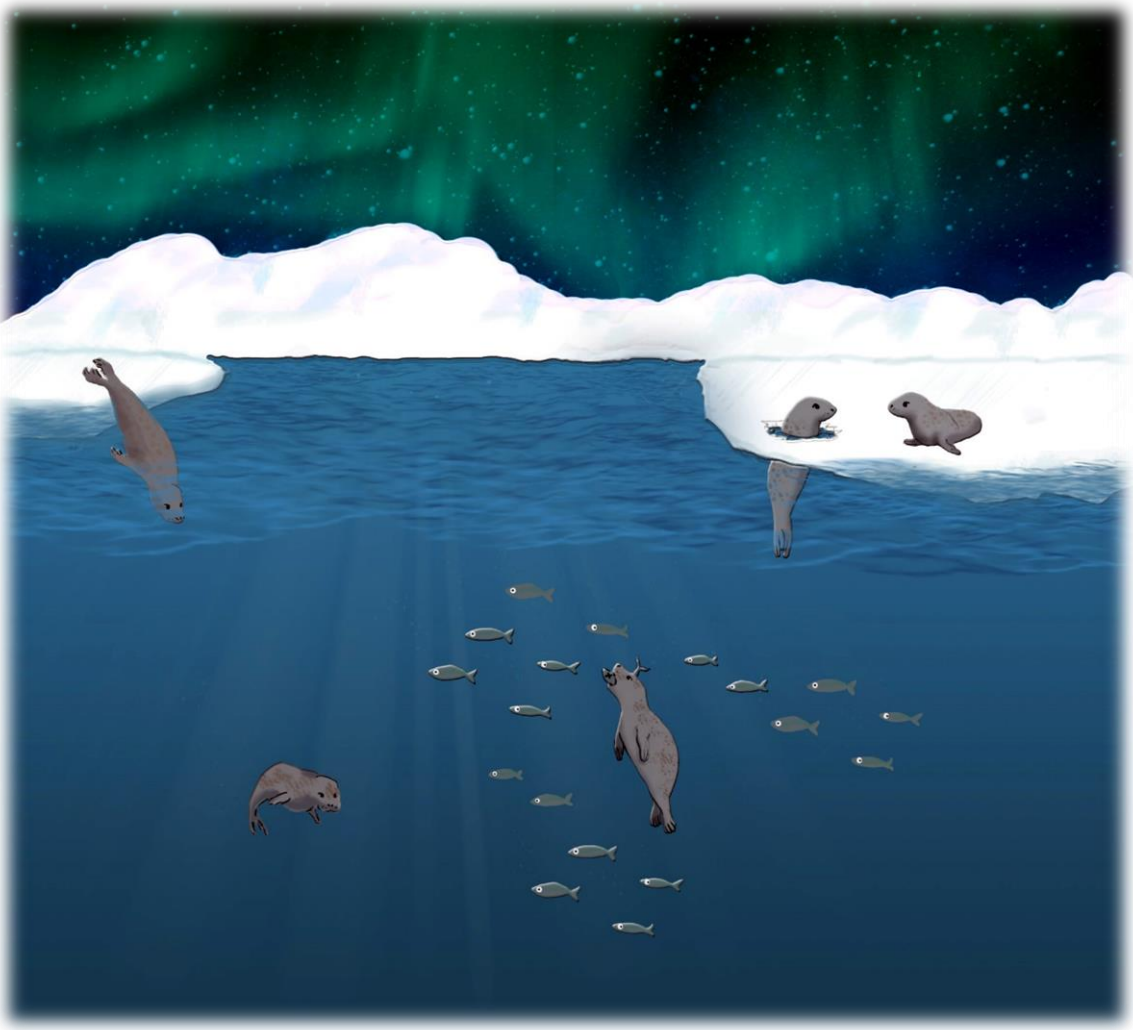
within a dive and quantifying foraging effort for each dive, particularly in species with complex dive behaviour such as the Weddell seal.

The second chapter (Paper 3) showed that by using an appropriate dive metric we could adapt the "hunting method" (developed in the first paper for high-resolution dives) to low-resolution dive profiles. The degradation of high-resolution dives into equivalent SRDL low-resolution dive profiles ensured a homogeneous comparison of the methods to identify and quantify foraging effort in the SES and Weddell seal datasets. The low-resolution foraging metric that best matched the high-resolution "hunting method" considered the time spent in low-resolution dive segments associated with a decreased vertical velocity (*i.e.* '$\text{hunting}_{\text{lowres}}$' segments). This suggests that despite degraded information typical of SRDL datasets, it is possible to detect and encapsulate most foraging activity in low-resolution dives. This requires to use a foraging metric that relies on the detection of changes in diving behaviour, rather than using pre-determined parts of the dive to distinguish between foraging and transit activity within a dive (*e.g.* assume the seal is in transit during descent and ascent phases and foraging during the bottom phase). Similar to the high-resolution study in Paper 2, our results were supported by independent prey capture attempts.

Assessing the influence of environmental features on marine predators' foraging behaviour rely on our ability to accurately detect foraging activity. In particular, a reliable metric of foraging activity is needed for time-depth datasets, which lack direct measures of feeding or prey encounter events and may be recorded at low resolution (such as those data from SRDLs). The foraging metrics developed in Paper 3 satisfy these needs and can easily be implemented into habitat selection/use studies (see Paper 5).

PART III

WEDDELL SEALS HABITAT USE DURING ANTARCTIC WINTER



Dessin de Coralie Chorin

A - Introduction

The aims of the following two chapters were to investigate the influence of environmental parameters on the winter diving and foraging behaviour of Weddell seals in two locations of East Antarctica.

Top predators adopt foraging strategies according to environmental features associated with the resources they need to ensure their reproductive success and survival (Krausman 1999; Stevick *et al.* 2002). Therefore, investigating the environmental parameters they respond to provide important information both on (i) the foraging behaviour adopted in a given habitat to meet their requirements and (ii) the type of prey targeted and/or ecosystem assemblages they rely on (*e.g.* Continental shelf, shelf break or oceanic assemblage). Finally, quantifying the importance of some environmental parameters to Weddell seal's foraging behaviour would help assessing the potential effects of environmental changes on Weddell seals in East-Antarctica. The set of abiotic parameters tested included the topography (Paper 4 and 5), the water masses (Paper 4), the light intensity (Paper 4) and sea-ice conditions (Paper 4 and 5). These specific environmental features were chosen for the following reasons. Regional topography appears to be a key parameter that drives the distribution of top predators, likely (but not only) via its influence on the hydrological circulation. In combination these two environmental parameters can enhance local productivity through nutrient enrichment (Prézelin *et al.* 2000; Nicol *et al.* 2006; Ducklow *et al.* 2007; Ribic *et al.* 2008). They can also act as a physical barrier (*e.g.* fronts, water masses boundaries) that aggregate primary and secondary producers attracting top predators' prey and/or facilitate prey accessibility (Burns *et al.* 2004; Zhou & Dorland 2004; Bost *et al.* 2009). Moreover, studies conducted during summer suggested that the bathymetry and oceanographic features influence

Weddell seals' diving behaviour (Plötz *et al.* 2001; Watanabe *et al.* 2003). Light intensity can influence visual top predators (such as the Weddell seal) in their search and pursue of a prey (Kooyman 1968, 1981; Davis *et al.* 1999). It can also drives nychtemeral migrations of some species targeted by top predators (*e.g.* krill, Silverfish) (Burns *et al.* 2008). Finally, sea-ice is a fundamental abiotic parameter for all life history traits of Weddell seals which is likely to influence: (i) the areas Weddell seals use as they need a stable ice to rest but not too thick to still be able to breathe, (ii) prey availability as it represents a substrate for ice-algae to grow. Several species rely on these epontic algae either directly (*e.g.* krill) or indirectly (*e.g.* Antarctic silverfish) (see Part I section "sea-ice dependant ecosystem"). Furthermore, Siniff *et al.* (2008) predicted changes in sea-ice conditions would likely affect Weddell seals.

The first chapter of this part (Paper 4) presents the first study on Weddell seal foraging ecology in Adélie Land. Before this study virtually nothing was known about the general movement patterns and diving behaviour of the Weddell seals from the Dumont D'Urville site. Moreover, we quantified the influence of abiotic parameters (bathymetry, bathymetric gradient, light intensity and sea-ice concentration) on their diving behaviour. Another original aspect of this study was the integration of the water masses in the habitat use models which has never been done before for the Weddell seals. In this study, several diving metrics were used from the low resolution dive profiles collected with SRDLs. We included in our analyses the dive depth and dive duration as well as an index of foraging effort. However, when this study was conducted, the method developed in Paper 2 and adapted to low-resolution dives in Paper 3 was not yet available. Thus, in this study dive foraging effort was quantified using the residuals of the bottom time (see details in Paper 4 and Bailleul *et al.* 2008).

The second chapter of this part (Paper 5) is a comparative study of the foraging ecology of Weddell seals from two sites in East-Antarctica. Taking a comparative approach allows to highlight important factors influencing foraging decisions that would not be apparent from studying a single site. We expanded the study conducted in Paper 4 by integrating all the SRDLs dive datasets available for the Weddell seals in East-Antarctica, including an additional year (2009) for DDU. We also developed a new approach to identify foraging activity considering the horizontal, temporal and vertical dimensions. We integrated the foraging effort index adapted (from the "hunting method" Paper 2) for low-resolution dive profiles (Paper 3) into a track-based method of ARS identification. Moreover, in this chapter we further investigated the influence of sea-ice on foraging effort and movement patterns by including more sea-ice variables (*e.g.* ice concentration, spatial variation of sea-ice and distance to ice edge) in the analyses. However, the SRDLs deployed on the Weddell seals from Davis only recorded water temperature which does not permit to identify water masses. Therefore to ensure a homogeneous comparison between the two study sites the hydrology was not considered in this chapter.

B - Paper 4

Deep-sea research part II (2013) **88-89:**23-33

Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behaviour

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1. Abstract

Studying the foraging strategies of top predators can provide information on both how animals interact with their environment and the distribution of their prey. We studied the winter foraging behaviour of Weddell seals in Adélie Land, East Antarctica, and the influence of abiotic parameters (bathymetry, hydrology, sea ice, light intensity) on their foraging behaviour. A total of six seals were fitted with Conductivity Temperature Depth Satellite Relayed Data Loggers (CTD-SRDL) at Dumont d'Urville (~67°S, 140°E) during the austral winters in 2007 and 2008. The tags transmitted positions and dive information over 169 ± 31 days, providing a total of 20400 dive profiles and 2350 CTD profiles. Significant environmental influences on seal diving behaviour and habitat use were detected. Seals dived deeper, longer and increased their foraging effort during the day than at night with intermediate values for twilight. During the winter season the maximum dive depth decreased in association with an increase in dive duration, but foraging effort was unchanged. Seals spent more time at the bottom of their dives in shallow waters associated with relatively smooth bathymetry and dominated by Antarctic Surface Water. Considering the whole winter, Weddell seals tended to favour enriched, warmer and less dense water masses following their seasonal appearance on the shelf (Antarctic Surface Water and Modified Circumpolar Deep Water). Our results are consistent with seals feeding primarily on *Pleuragramma antarcticum* during winter, tracking their vertical diel migrations and foraging in areas associated with bathymetric and hydrographic features likely to concentrate prey patches.

Keywords: Weddell seals, foraging behaviour, Austral winter, telemetry, oceanography, marine ecology.

2. Introduction

The Antarctic margin is highly productive in particular areas, such as the coastal margins of the Antarctic continent, and coastal polynyas (Burns *et al.* 2004). This primary production is generally linked to the seasonal mixed layer that forms as sea ice melts each spring (Chapman *et al.* 2004) and is associated with a high biomass of top predators, such as seabirds and marine mammals (Ainley *et al.* 1998; Burns *et al.* 2004; Ducklow *et al.* 2007). However, the nature of the trophic links between physical characteristics of the environment and biological production, zooplankton and resource distribution, and how these impact predator foraging performance remains poorly known. During the Antarctic winter, predators face darkness, reduced productivity, increased ice cover, modified hydrographical regimes and associated changes in prey abundance and availability (Burns *et al.* 2004; Biuw *et al.* 2007).

Located at the top of the food web, seabirds and marine mammals can integrate the temporal and spatial variations of the lower trophic levels (Hindell *et al.* 2003). Their movement patterns and diving behaviour reflect to some extent the distribution and availability of their prey (Biuw *et al.* 2007; Bost *et al.* 2008; Durant *et al.* 2009). Recent developments in telemetry technology allow us to simultaneously record data on horizontal and vertical movements of predators, and high quality data on the *in situ* physical environment in which they inhabit (Rutz & Hays 2009; Williams *et al.* 2011). This is particularly useful to investigate how top predators use the physical marine environment and how these parameters can influence their foraging strategies (Charrassin & Bost 2001; Fedak 2004; Biuw *et al.* 2007, 2010).

Weddell seals (*Leptonychotes weddellii*) are the most southerly breeding seal and the only predator, along with the Emperor penguin (*Aptenodytes forsteri*), to inhabit sea-

ice during the whole year (Burns & Kooyman 2001). Weddell seals forage under the sea-ice, and also use it as a substrate to breed (with female giving birth on the ice) and moult (Cornet & Jouventin 1980; Castellini *et al.* 1992a). The Weddell seal is the second deepest phocid diver of the Southern Ocean after the southern elephant seal attaining more than 600 m in the Ross sea (Castellini *et al.* 1992a). The Weddell seals are opportunistic predators feeding mainly on fish, but also on cephalopods and crustaceans, in proportions that vary according to age, location and season (Lake *et al.* 2003). Weddell seal foraging behaviour has been extensively studied in summer and studies conducted in the Wedell Sea (Plötz *et al.* 2001) and the Ross Sea (Watanabe *et al.* 2003) suggest that there was an influence of summer oceanographic conditions and physiography on the Weddell seals diving behaviour. Winter movements and diving behaviour have been studied at several Antarctic locations, including the Ross sea (Castellini *et al.* 1992a; Testa 1994b; Burns & Kooyman 2001), and in Prydz Bay (Lake *et al.* 2005, 2006). However, winter studies are still few and the interaction between Weddell seals foraging strategies and their environment remains poorly known.

Here, we present the first study on Weddell seal foraging ecology in Adélie Land, characterizing their winter diving behaviour and movement patterns. The coastal area off Adélie Land is associated with complex bathymetry and hydrology, with inshore depressions and canyons, and is influenced by several water masses (Williams & Bindoff 2003; Marsland *et al.* 2004). We aimed to determine if the winter movements and diving behaviour of Weddell seals were influenced by key physical parameters of their marine habitat, including bathymetry, seafloor rugosity, sea ice concentration and water masses. Bathymetry features can influence the hydrological regimes of an area, which could enhance ecosystem productivity (Tynan 1998; Prézelin *et al.* 2000) and can also serve as prey refuges (Zhou & Dorland 2004). Thus, we expected Dumont D'Urville seals to select

more productive and shallow waters associated with higher prey availability and accessibility; and also to forage in areas associated with lighter sea ice concentrations in order to facilitate their surface access. We also investigated the influence of decreasing light intensity as winter advanced on their diving behaviour and use of the water column as they were likely to adapt their diving behaviour to the diel and seasonal migrations of their prey.

3. Materiel and methods

3.1 Animal handling and tagging

Eight adult female Weddell seals were captured in February after their annual moult at Dumont d'Urville (66°40' S, 140°00 E) during two successive summers, in 2007 (n = 3, 337 ± 16 kg, 238 ± 5 cm) and 2008 (n = 5, no mass data, 235 ± 8 cm). Each seal was fitted with a CTD-SRDL (Sea Mammal Research Unit [SMRU], University of St. Andrews, Scotland). The seals were approached on the ice by foot and temporarily restrained with a head bag and an intravenous injection of Zoletil (1:1 mixture of tiletamine and zolazepam), at a dosage of 0.5 $mg.kg^{-1}$, was administered (Wheatley *et al.* 2006; Andrews-Goff *et al.* 2010). Initial dosages prior to capture were estimated for all seals. The CTD-SDRL was attached to the head with the antenna facing forward using a two component industrial epoxy (Araldite AW 2101). The seal was observed during recovery from anaesthesia and allowed to enter the water when no longer sedated. For the purpose of this paper, six seals out of eight (n= 3 in 2007 and n=3 in 2008) had sufficient data covering the austral winter season to be included in the analyses.

3.2 Data collected from the tags

The CTD-SRDLs measure standard oceanographic data and transmit a simplified profile of the data along with the seal position through the Argos satellite system (for more details on the CTD-SRDLs, see Boehme *et al.* 2009). Hydrographic data were recorded every second during the ascent phase of the dives. Temperature and conductivity were measured with resolutions of 0.006°C and 0.004 $mS.cm^{-1}$ S, respectively. Salinity was calculated on board before transmission from conductivity measurements. The tags were

calibrated before deployment and hydrographical data were corrected for pressure effect as described in Roquet *et al.* (2011). After correction, pressure (P), temperature (T) and salinity (S) accuracies were 2 dbar, 0.01-0.02°C, and 0.03, respectively (Charrassin *et al.* 2008; Roquet *et al.* 2011). The two deepest CTD profiles were kept for each six hours period and transmission of those profiles was attempted when the seal was at the surface. Transmission constraints (narrow bandwidth of the Argos satellite system and limited seal surface time) resulted in a reduction of the T and S profiles to 20 data points selected as described in Roquet *et al.* (2011) and in an average of two complete CTD profiles transmitted per seal per day (Table 4.2).The SDRLs were programmed to record dive depth and time every 4s during diving, from which dive start and end time, dive duration and post-dive surface interval were determined. Uplinks were attempted every 40s when the seal was surfacing. For each dive, tags transmitted only the four main inflexion time-depth points where the dive shape changed most rapidly.

3.3 Argos Kalman filtering

Argos location accuracy depends on the duration and number of transmissions between satellites and SDRLs. For each Argos location, a location class (3, 2, 1, 0, A, B and Z from the more accurate to the less accurate class) is assigned giving information on the number of satellite transmissions and the location accuracy (Patterson *et al.* 2010; Service Argos 2010). Approximately 40 % of the locations of our study were associated with an estimated error (from less than 250 m to more than 1500m, classes 3 to 0), 50 % had no accuracy estimation (classes A and B) and 10 % were invalid (class Z). Argos locations were filtered using a combination of heuristic speed filtering and a Kalman filter that accounted for location error of the different Argos location classes as described in

Patterson *et al.* (2010). Kalman smoothed locations were provided at the time of each original Argos location, along with a bivariate Gaussian error ellipse describing the uncertainty around each location (Patterson *et al.* 2010). All further analyses were then conducted on the corrected, Kalman filtered positions.

3.4 Bathymetry and sea-ice data

We used two bathymetry datasets according to their spatial resolution. Fine-scale bathymetry (Beaman *et al.* 2011; 500 m per cell grid) was used for analytical purposes (http://data.aad.gov.au/). The GEBCO_08 database (30 sec per cell grid (≈ 1 km)) was used for graphical purposes only (http://www.gebco.net/). Using the Beaman *et al.* (2011) bathymetry, an index of seafloor rugosity was calculated as the variance of bathymetric data within 2 x 2 km grid cells, thus including 16 bathymetry data points (Burns *et al.* 2004). Bathymetry was extracted at each Kalman smoothed location using the R package *sp* (R development Core Team, function *overlay*; Pebesma & Bivand 2005; Bivand et al., 2008). A weighted mean of bathymetric data was then calculated and associated with each location by weighting each bathymetric value in the associated Kalman error ellipse (Appendix S4.1). For bathymetric gradients, the mean cell values were associated with each Kalman smoothed dive location (library *sp*, function *overlay*).

Sea ice concentration was extracted from AMSR-E daily sea ice concentration images (http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html). Each "pixel" in the image has an allocated ice concentration (from 0 to 100 %) and is equal to 5.95 × 6.57 km. As for bathymetry, ice concentration was extracted at each Kalman smoothed location using the R package (library *sp*, function *overlay*) and a weighted mean of ice concentration was calculated and associated with each corrected location (Appendix

S4.1). For further analysis ice concentrations were classified into three categories based on their frequency distribution: light concentration ([ice] < 20 %), medium concentration (20 ≤ [ice] ≥ 80 %) and extensive concentration ([ice] > 80%).

3.5 Hydrological data

To characterize the different water masses sampled by the seals, we calculated additive variables based on Fofonoff & Millard (1983) definitions and using R package *oce* (R development Core Team; Kelley, 2012): potential temperature (θ °C, function *sw.theta*), potential density (σ_0 kg.m^{-3} , function *sw.rho*) and the density at 4000 m (σ_4 kg.m^{-3} function *sw.rho*). Key water masses (Antarctic Surface Water, modified Circumpolar Deep Water, Shelf Water and Ice Shelf Water) were discriminated using criterions defined in Orsi & Wiederwohl (2009) and Williams *et al.* (2008) and modified for our dataset (Table 4.1): we used density at 4000 m which is the closest to neutral density (Orsi & Wiederwohl 2009) and for which isopycnals were the best adapted to our dataset. To obtain continuous T and S vertical profiles, a linear interpolation was applied between the 20 data points of each profile, considering the mean interval between two data points for all the profiles (5.2 ± 0.2 m) to avoid addition of non-available data (Fox & Brown 1965). Following this, a six meter interpolation step was used for potential temperature, salinity and density profiles. A water mass was then assigned to each interpolated data point.

The bottom phase of dives (time spent below 80 % of the maximum depth) is thought to be the period of the dive devoted to foraging (Watanabe *et al.* 2003; Mitani *et al.* 2004; Burns *et al.* 2008). To identify the main water mass used by the seals while hunting for prey, we determined the water mass encountered during the bottom phase of each dive. Because T and S data were not available for all dives, we first associated with

each dive the closest CTD profile in time collected by the same individual (average time difference between the dive and CTD profile 243 ± 2 $_{(SE)}$ min). We then extracted from the associated CTD profiles of each dive the water masses present at the different depths included in the bottom phase, and we defined the most frequent water mass encountered as the bottom phase water mass for that dive.

Table 4.1. Definitions of the water masses determined from CTD-SLDR temperature and salinity measurements collected by female Weddell seals during Austral winter 2007 and 2008.

Water Mass	Temperature (°C)	Salinity	Density at 4000 m ($kg.m^{-3}$)
AASW (Antarctic Surface Water)			< 45.92
AASW/MCDW (AASW / Modified Circumpolar Deep Water)			≥ 45.92 et < 46.16
MCDW	> - 1.85		≥ 46.16 et < 46.27
MSW (Modified Shelf Water)	> - 1.85		≥ 46.16
LSSW (Low Salinity Shelf Water)	≤ - 1.85	< 34.62	≥ 46.16
HSSW (High Salinity Shelf Water)	≤ - 1.85	≥ 34.62	≥ 46.27
ISW (Ice Shelf Water)	≤ - 1.93		

3.6 Behavioural data

In Weddell seals, short and shallow dives may be associated to non-foraging activities, such as social, resting and transit behaviours (Testa 1994b). In order to separate those dives from foraging dives, we examined the frequency distribution of diving depths (Burns *et al.* 2004). Dive depths and durations were bi-modally distributed, with a first group indicating dives ≤ 25 m with a modal duration of < 1 min and a second with dives > 25 m. Dives < 25 m were then excluded from further analysis (36 % of all the dives).

For each dive, the difference between the bathymetry at the corrected dive position and the maximum dive depth was calculated (hereafter named "depth difference"). We found that 36 % of maximum dive depths were greater than bathymetry at the same position, probably as a result of combined errors in bathymetry and seal positions. Depth difference was normally distributed with a mode comprised between -30 and 30 m, suggesting that this mode corresponds to seals foraging at the sea bottom, and that depth difference lower than -30 m indicated bathymetry and/or seal position errors. Dives deeper than the bathymetry by more than 30 m were therefore removed from the dataset (25 % of the dives > 25 m). Based on these observations, dives > 25 m were separated in two types: 1) benthic dives with maximum depth comprised between [bathymetry – 30] m and [bathymetry + 30] m; and pelagic dives with maximum depth shallower than [bathymetry – 30] m.

Dive parameters included maximum dive depth, dive duration, bottom-time (bt, time spent below 80 % of the maximum depth). Since bottom time is strongly related to dive depth and dive duration, we calculated the bottom time residuals (*Rbt*, Bailleul *et al.* 2008) as a proxy of foraging effort, with positive and negative residuals indicating a greater or lower foraging effort than predicted for a particular dive depth and duration, respectively. To examine the effect of light intensity on the seal diving behaviour, the sun angle above or below the horizon according to local time of each dive was used to divide the day into three periods: day (sun above horizon), twilight (sun between 0 to 12° below horizon), night (sun > 12° below horizon) using the R package *maptools* (function *solarpos*; Burns *et al.* 2008; Bivand & Lewin-Koh 2014).

2.7 Statistical analysis

To determine the relationships between the temporal (year, day of year considered after as winter advance, light intensity) and environmental parameters (bathymetry, seafloor rugosity, hydrographical habitat, ice concentrations) and diving behaviour (dive duration, maximum diving depth, Rbt), we fitted a series of generalized linear mixed effect models (GLMMs) using the R software package *nlme* (R development Core Team, function *lme*; Pinheiro *et al.* 2007) following the steps described in Zuur *et al.* (2009). First, variables were transformed prior to analyses to correct for non-Gaussian distributions (log transformation for maximum diving depth, seafloor rugosity and bathymetry). The year, light intensity and hydrographical habitat variables were expressed as factors in the models. Non-colinearity (coef. < 0.5) was verified between continuous variables using Pearson correlation (Zuur *et al.* 2009).

To obtain an initial idea of the shape of relationships between the response variables (diving behaviour parameters) and the predictor variables (temporal and environmental parameters), we first considered a full generalized additive mixed model (GAMM, R software package *mgcv*, R development Core Team, function *gamm;* Wood 2006, 2011) with all environmental covariates included for each response variable. Based on the GAMM outcomes, we then fitted GLMMs, (library *nlme*, function *lme*), with individual included as a random effect to account for inter-individual variability. An auto-correlation term was also added to each GLMM to account for temporal correlation in the data (Zuur *et al.* 2009; Bestley *et al.* 2010). Model selection was made using the likelihood ratio test, based on maximum likelihood (ML), starting from a full model with fixed effects (temporal and environmental variables) retained only if they improved the fit ($p < 0.05$, Zuur *et al.* 2009; Bestley *et al.* 2009). We verified that the most parsimonious model was also the

model with the lowest Akaike's Information Criteria (AIC) (Zuur *et al.* 2009; Bestley *et al.* 2010). Finally each optimal model was fitted with the Restricted Maximum Likelihood Estimation (REML) method and residuals were plotted to verify their homogeneity and validate the GLMM (Zuur *et al.* 2009). Results given by GLMMs for factors were calculated in reference to the first factor (example: for light intensity, results for night and twilight were given in comparison to day, see results).

4. Results

4.1 Tag performance, foraging areas and diving features of Weddell seals in winter

The six tags transmitted data for periods of 181 to 241 days (213 ± 11 $_{(SE)}$ d.) covering late summer, autumn and winter from late February to mid October. With 2 ± 0.1 profiles transmitted each day, the seals collected a total of 2350 CTD profiles. Simultaneously, 20400 dives were recorded with 14 ± 1 dives per day (Table 4.2).

The mean distances from the colony over the study period were 34 ± 3 $_{(SE)}$ km (max: 107 km, n=6) showing an overall coastal distribution of the seals, which travelled 3 ± 0.4 km per day (max: 38 km.day^{-1}, n=6) on average (Table 4.2, Fig. 4.1 to 4.2). Areas explored were relatively stable among years with seals generally travelling west or north before heading east over winter (Fig. 4.1). Seals primarly used relatively shallow coastal waters of less than 280 m (237 ± 1 m, max: 1290 m, n=6, Fig.4.1 to 4.2) although also explored waters of the canyon underneath the Astrolabe Glacier, where dives down to 904 m were recorded, which is to our knowledge the maximum for this species (Fig. 4.2). Dives were predominantly associated with low seafloor rugosity (calculated on 4 km^2 cell, 32 ± 0.2 m, max: 229 m, n=6) where bathymetry varied less than 56 m and predominantly in ice concentrations of more than 80%. Dives were performed during day (34%), during night (39%) and during twilight (28%). The mean maximal dive depth was 130 ± 20 m (n=6) but ranged from 426 to 904 m according to individual (Table 4.2, Fig. 4.2). Pelagic dives represented 63% of the dives and were associated with deeper water, compared to benthic dives (37%), which were associated with shallower waters (289 ± 2 m and 150 ± 1 m, respectively, t-test: $p < 0.001$). Mean dive duration and mean bottom time duration were

14 ± 0.5 min and 8 ± 0.3 min, respectively (n = 6). Bottom time represented 57 ± 2 % (n=6) of the corresponding dive duration (Table 4.2).

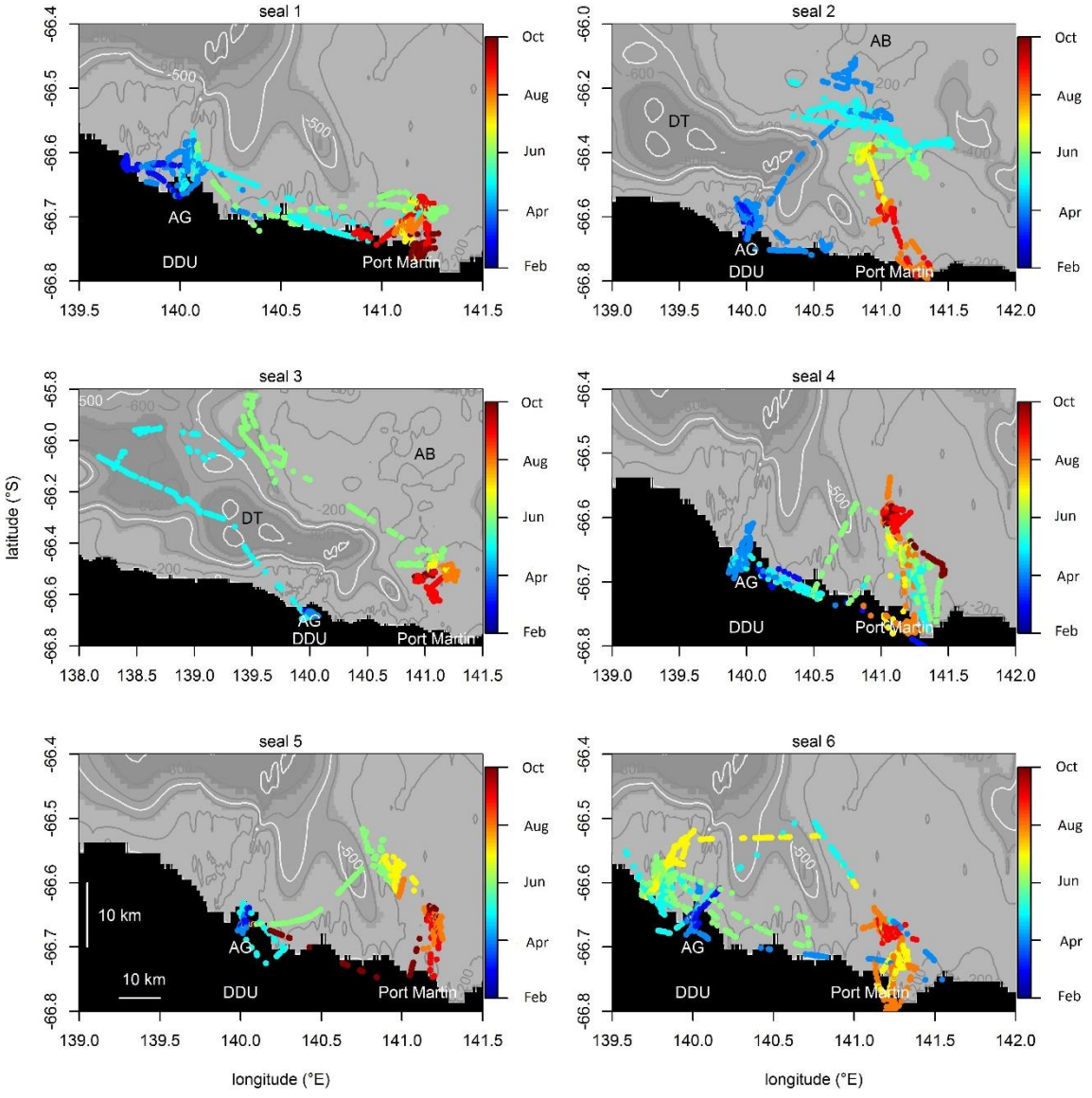

Figure 4.1. Tracks of CTD-SRDL equipped Weddell seals from Dumont d'Urville foraging during winter 2007 (seal # 1 to 3) and winter 2008 (seal # 4 to 6) after correction of Argos locations with a Kalman Filter. The colour scales indicate the month (by month number). AB: Adélie Bank, AG: Astrolabe glacier, DDU: Dumont D'Urville colony, DT: D'Urville trough. Note that scales are different according to individual movements.

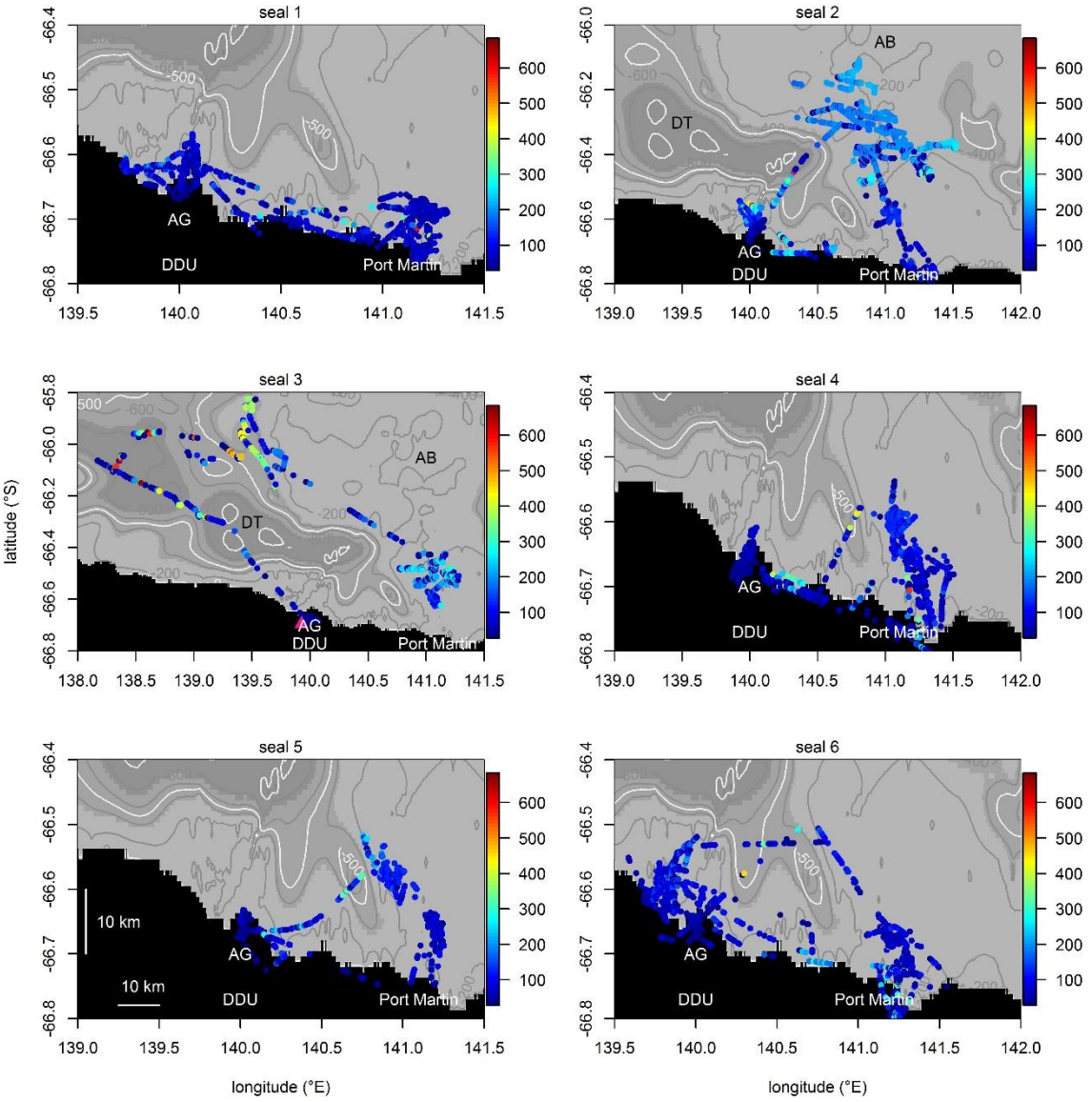

Figure 4.2. Tracks of CTD-SRDL equipped Weddell seals from Dumont d'Urville foraging during winter 2007 (seal # 1 to 3) and winter 2008 (seal # 4 to 6) after correction of Argos locations with a Kalman Filter. The colour scales indicate the maximal depth (m).

Table 4.2. Basic information on movements and diving behaviour of Weddell seals outfitted with SDRL tags at Dumont d'Urville in 2007 and 2008. Means are expressed ± SE, maximum values are presented below means. The distance to the colony is the mean distance from the colony calculated from each position. The distance per day, is the distance travelled between the first and the last locations of each day.

Seal ID	Mass (kg)	Size (cm)	Date of deployment	Duration of deployments (days)	Distance to the colony (Km)	Distance per day (Km)	Number of dives	Number of dives Per day	Number of CTD profiles	Number of CTD profiles per day	Mean maximal depth (m)	Duration (min)	Bottom time (min)
Seal 1	364	246	20/02/07	241	31 ± 0.3 57	2 ± 0.2 25	4377	18 ± 0.8 60	407	2 ± 0.06 4	82 ± 1 584	14 ± 0.1 96	9 ± 0.1 56
Seal 2	307	237	20/02/07	182	39 ± 0.2 75	4 ± 0.4 34	3925	16 ± 1 88	407	2 ± 0.06 4	165 ± 1 604	13 ± 0.1 39	8 ± 0.1 35
Seal 3	339	230	21/02/07	208	43 ± 0.1 107	3 ± 0.3 33	3135	13 ± 0.7 54	424	2 ± 0.06 4	207 ± 3 904	14 ± 0.1 45	7 ± 0.1 37
Seal 4	-	250	23/02/08	235	37 ± 0.5 66	2 ± 0.3 38	3255	13 ± 0.7 42	388	2 ± 0.06 4	124 ± 2 804	14 ± 0.1 85	8 ± 0.1 61
Seal 5	-	223	22/02/08	233	27 ± 0.02 55	1 ± 0.1 14	2723	11 ± 0.5 45	409	2 ± 0.1 4	112 ± 2 544	15 ± 0.1 40	9 ± 0.1 32
Seal 6	-	232	21/02/08	181	28 ± 0.3 68	3 ± 0.4 32	2983	12 ± 0.7 46	315	2 ± 0.6 4	88 ± 1 524	12 ± 0.1 37	7 ± 0.1 22

4.2 Use of hydrographic environment

Based on the criterions defining water masses (Table 4.1), a total of seven water masses were encountered during the dive bottom phase of the Weddell seals tagged in this study (Fig. 4.3). AASW and ISW were encountered only in 2007 (Fig. 4.5). Overall, all individuals except seal # 5 sampled the five other water masses, but spent most of their bottom time in MCDW (46%, Fig. 4.4). According to individual, bottom time was predominantly spent in MCDW (54 to 78 % of their bottom time, n=4), LSSW (31 %, n=1) and MSW (30 %, n=1), with MCDW and MSW present in the areas seals sampled throughout the whole season (Fig. 4.4, Fig. 4.5). LSSW (Mar. to Sep.), HSSW (May. to Sep.) and ISW were sampled during most of the period on the Adélie Bank but in lower proportions (Fig. 4.5). AASW and AASW/MCDW were representative of the late summer season and were essentially used by the seals near the colony at the beginning of their trip (Fig. 4.5).

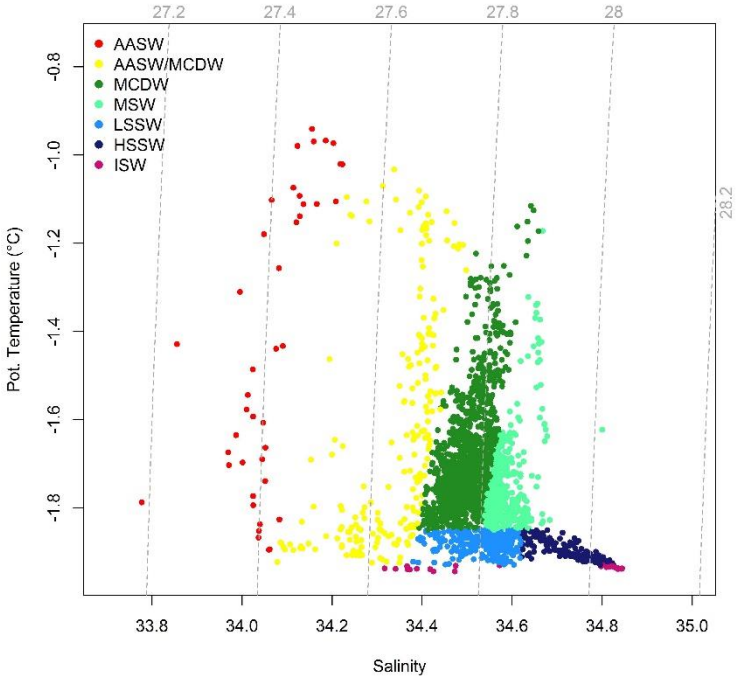

Figure 4.3. T-S diagram representing all water masses sampled during the entire winter trip of all the seals during the bottom phase of their dives.

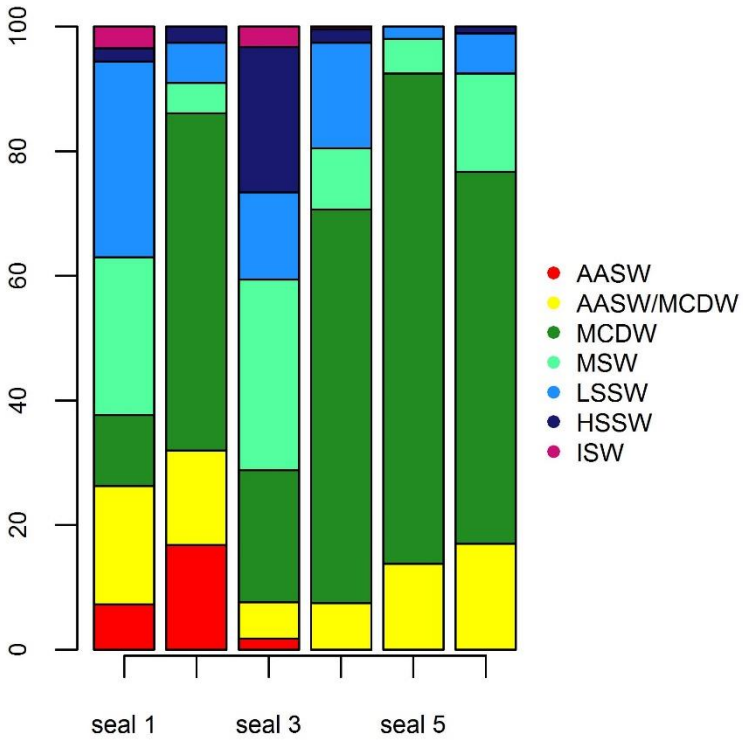

Figure 4.4. Bottom time spent in each water mass sampled during the winter trip of each individual expressed as a percentage of the bottom time spent in all water masses encountered by each seal.

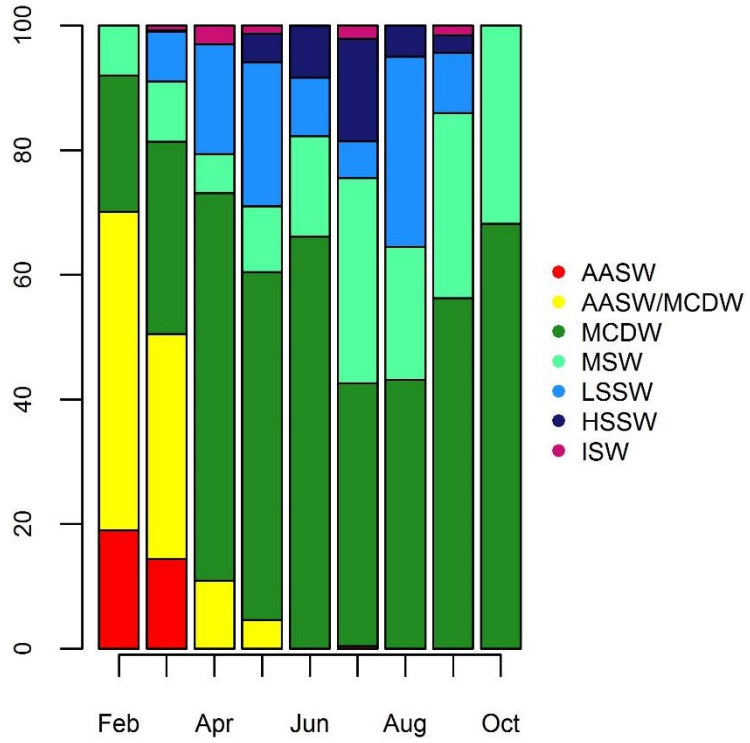

Figure 4.5. Water masses sampled during one month by all individuals during the bottom phase of their dives expressed as a percentage of all water masses encountered each month.

4.3 Influence of environmental and temporal factors on foraging behaviour

We studied the influence of physical (bathymetry, seafloor rugosity, hydrological habitat and sea ice concentration) and temporal (day of year and light intensity) parameters on three variables of the Weddell seal diving behaviour, comprising maximum dive depth, dive duration and a proxy of foraging effort: bottom time residuals. For all these behavioural parameters, no significant effect of sea-ice concentration was detected.

4.3.1 Maximum dive depth

The most parsimonious GLMM describing maximum dive depth included physical (bathymetry, seafloor rugosity and water masses) and temporal (advance of winter, light intensity) variables (Table 4.3). Seals dived deeper when bathymetry increased (coef. 0.25 ± 0.01 $_{(SE)}$, $p < 0.0001$, Table S4.1) but dived at shallower depth when the bathymetry was more variable (coef. - 0.05 ± 0.01, $p < 0.0001$, Table S4.1). Maximum dive depths were shallower during night (84 ± 2 m,; GLMM coef. - 0.35 ± 0.02, $p < 0.0001$), and twilight (98 ± 7 m; GLMM coef. - 0.14 ± 0.02, $p < 0.0001$) compared to day (121 ± 12 m) and overall maximum dive depth decreased with the advance of winter (coef. - 0.001 ± 0.0002, $p < 0.01$) (Fig 4.6a, Table S4.1). Nocturnal maximum dive depth did not vary much over the winter months with values ranging from 73 ± 4 m to 92 ± 3 m. Both day and twilight maximum dive depth showed a more varied pattern, with values increasing from February (day: 121 ± 5 m, twilight: 78 ± 4 m) to May (day: 180 ± 4 m, twilight: 129 ± 3 m) and then decreasing until October (day: 84 ± 2, twilight: 78 ± 2) (Fig. 4.6 a).

4.3.2 Dive duration

The most parsimonious GLMM describing dive duration included two physical (bathymetry and water masses) and two temporal parameters (day of year, light intensity) (Table 4.3). Individuals dived for longer durations when bathymetry increased (coef. 29.86 ± 7.31 $_{(SE)}$, $p < 0.0001$) and with the advance of winter (coef. 0.52 ± 0.11, $p < 0.0001$) (Table S4.1). Dive duration was shorter during night (728 ± 25 sec; GLMM coef. - 124.79 ± 11.80, $p < 0.0001$) and twilight (776 ± 20 sec; GLMM - 37.86 ± 12.48, $p < 0.01$) than during the day (808 ± 23 sec) (Fig. 4.6 b, Table S4.1). The oposite occured in February and March as nocturnal dives were longer (797 ± 32 sec.) than the ones performed during day

(757 ± 48 sec.) and twilight (740 ± 11 sec., Fig. 4.6 b). Overall dive durations decreased from February (day: 805 ± 18 sec., twilight: 751 ± 20 sec., night: 829 ± 31 sec.) to April-May (day: 698 ± 11sec., twilight: 705 ± 16 sec., night (Apr.): 625 ± 8 sec.) then increased until September-October (day: 893 ± 39 sec., twilight: 867 ± 45 sec.,night (Sep.) : 835 ± 16 sec.) (Fig. 4.6 b).

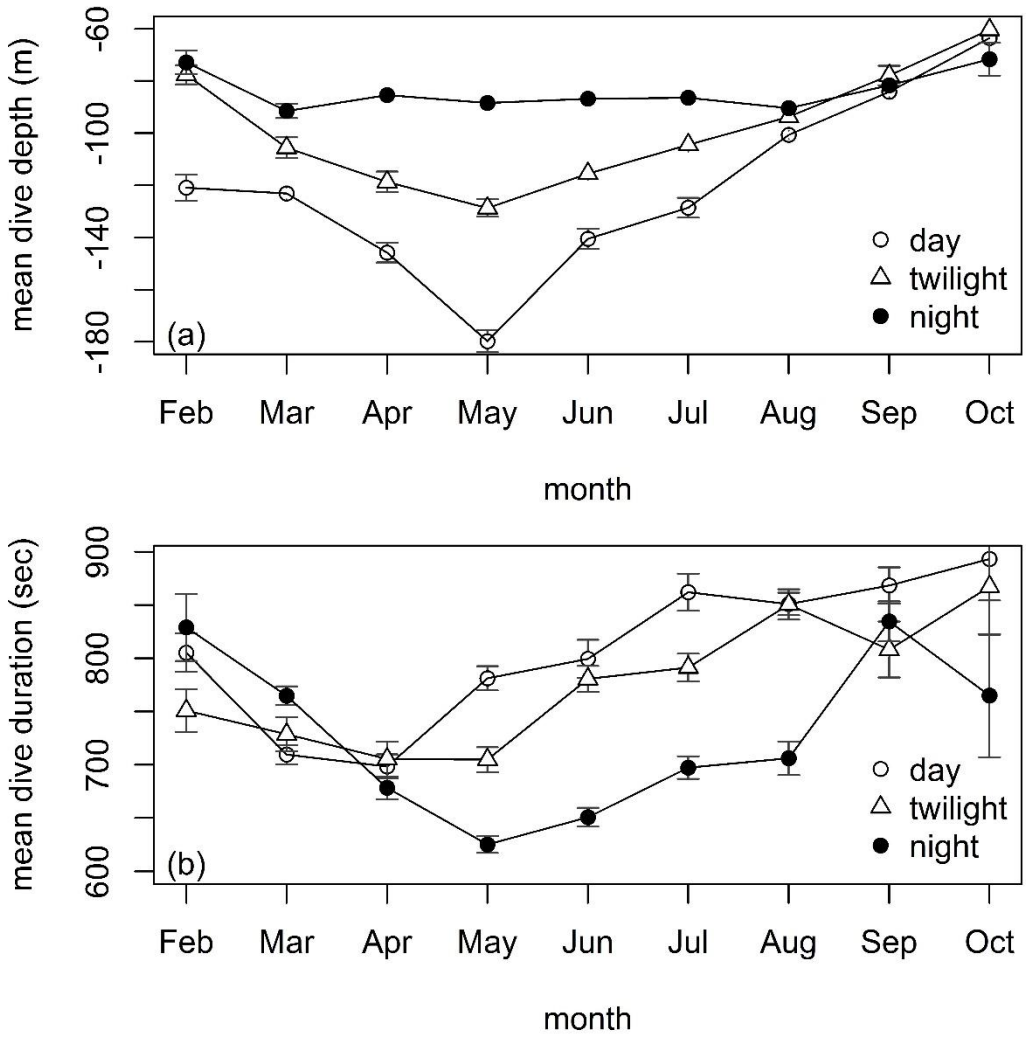

Figure 4.6. Monthly mean (± SE) of maximum dive depth (m) (A) and dive duration (sec) (B), according to different light intensities: day (blank circle), night (dark circle) and twilight (blank triangle). Data were pooled for 2007 and 2008.

4.3.3 Bottom time residuals

The most parsimonious GLMM describing bottom time residuals included two physical (seafloor rugosity and water masses) and one temporal (light intensity) parameter (Table 4.3). Bottom times were relatively shorter in a more variable bathymetry (- 3.69 ± 1.17 $_{(SE)}$, $p < 0.01$, Table S4.1), Hydrography also influenced Rbt which was more negative in all the water masses compared to AASW (ASSW/MCDW coef. -61.26 ± 5.91; MCDW coef. -70.14 ± 13.13; MSW coef. -71.78 ± 14; LSSW coef. -85.38 ± 14; HSSW coef. -84.32 ± 16.64; ISW coef. -92.96 ± 24.29; $p < 0.0001$ for all) meaning that bottom time was longer than expected in AASW (Table S4.1). Bottom time was shorter than expected at night and twilight (coef. – 20.79 ± 5.53, $p < 0.001$ and – 16.66 ± 5.91, $p < 0.01$, respectively) than during the day (Table S4.1).

Table 4.3. The most parsimonious model structure for GLMMs investigating relationships between dive depth, dive duration and residual bottom time and environmental and temporal parameters in six female Weddell seals.

Model	AIC	LL	Observations (n)	Individuals (n)
DEP ~ BAT + SLP + DOY + DN + WM	**6205.32**	**- 3087.66**	**4171**	**6**
DUR ~ BAT + DOY + DN + WM	**59468.19**	**- 29720.09**	**4171**	**6**
RBT ~ SLP + DN + WM	**53334.58**	**- 26654.29**	**4171**	**6**

5. Discussion

This study was conducted by collecting concurrent data on seal diving behaviour and their hydrological environment during winter using SDRL-CTD tags. This represents a significant advance over similar studies in two ways. Firstly the environmental characteristics encountered by seals were collected at a scale appropriate to their movements, being collected by the seals themselves as they moved through the environment. In contrast earlier studies used remotely sensed data with spatial resolutions that differ considerably from the movements of the seals. Secondly we were able to measure ocean properties throughout the water column, which for deep diving seals means that conditions encountered at depth, rather than surface values can be included in models. We also simultaneously modeled these physical variables with temporal factors to obtain an integrated assessment of the factors that influence Weddell seal diving behaviour. Individuals used the shelf area of Dumont D'Urville associated with high sea-ice concentration, shallow waters, relatively smooth seafloor and MCDW. As observed in other locations, Dumont d'Urville seals used the entire water column to forage, alternating between benthic and pelagic dives (Plötz *et al.* 2001; Hindell *et al.* 2002). The maximum dive depths and durations observed were similar to over winter studies (Castellini *et al.* 1992a). However, this study documented the deepest (904 m) and longest (96 min) dives ever recorded for Weddell seals.

5.1 Effect of winter advancement and circadian light cycle on diving patterns

Winter is a critical time for female Weddell seals since they are gestating and must also lay down energy reserves to sustain them during the subsequent pup rearing period of fasting (Cornet & Jouventin 1980; Castellini *et al.* 1992a; Wheatley *et al.* 2008). Reproductive demands require that, they must store energy and gain weight during winter to ensure reproductive success and survival. During winter, Weddell seals face an increase in sea-ice cover and modified hydrographical regimes affecting the availability and distribution of prey (Burns *et al.* 2004; Bailleul *et al.* 2007). Overall effect of the advancing winter season was a decrease in the maximum dive depth associated to an increase of dive duration but with no effect on the foraging effort as estimated from residual bottom times. These results suggest that seals were increasing the transit phases of their dives with the advance of winter. It has been suggested that within the radius of each breathing hole, prey resources can become depleted especially if several seals are foraging in the same area (Kooyman 1975). When faced with local resource depletion, Weddell seals may engage in long and shallow exploratory dives under sea-ice to find new holes or cracks associated with new patches of prey.

Female Weddell seals dived deeper, longer and spent relatively more time at the bottom of their dives during the day than at night with intermediate values for twilight. Variation in light intensity is an inherent effect of the winter season during which day duration decreases from 14 hours in March to 2 hours in July (Andrews-Goff *et al.* 2010) and when relatively thick ice and snow reduce under ice irradiance to less than one percent of the surface light level (Castellini *et al.* 1992a). Weddell seals are visual predators and use the under-ice surface for backlighting when foraging (Davis *et al.* 1999), therefore

diurnal and seasonal variations of light intensity would inevitably affect their foraging behaviour.

Light intensity also has a direct influence on prey distribution in the water column. (Burns *et al.* 2004, 2008). Weddell seals feed both on pelagic prey such as *Pleuragramma antarcticum* and squids, and benthic prey such as *Trematomus* fish species and invertebrates (Green & Burton 1987; Castellini *et al.* 1992a; Burns *et al.* 1998). Stable isotope analysis of blood collected from Weddell seals at Dumont D'Urville in winter revealed a pelagic diet of high trophic level, consistent with consumption of *P. antarcticum* (Y. Cherel, pers. com.), as observed in other locations (Green & Burton 1987; Castellini *et al.* 1992a). *P. antarcticum* aggregates in shoals distributed in different parts of the water column according to life cycle stage and time of the day, migrating vertically in the water column in direct relation to light intensity. Fuiman *et al.* (2002) suggested that during winter *P. antarcticum* could be distributed in the top 90 meters of the water column, which also corresponds to the most frequent dive depths recorded for pelagic dives in this study (63 % of the dives). Our study suggests that Weddell seals alter their foraging behaviour to track the circadian migrations of their prey. Diurnal and seasonnal shift in foraging patterns consistent with foraging on vertically migrating prey has been observed in other marine predators such as Antarctic fur seal (*Arctocephalus gazella*) and crabeater seals which are predominantly krill feeders (Croxall *et al.* 1985; Burns *et al.* 2008).

5.2 Habitat selection and influence of the environment on foraging behaviour

Energy balance is the net result of the costs associated with foraging and the energy derived from prey, and this is crucial for air-breathing divers, which are limited by their

metabolism and aerobic dive limit to find prey (Kooyman *et al.* 1983; Williams *et al.* 2004). Predators can increase foraging success by foraging selectively in habitats where prey is more abundant or easier to capture in regard to environmental features (Leibold 1995; Chapman *et al.* 2004; Ducklow *et al.* 2007).

5.2.1 Sea-ice

Seasonal changes in sea-ice cover affect species distribution and particularly for air-breathing predators (Massom & Stammerjohn 2010). Weddell seals in Adélie Land predominantly used highly concentrated ice during winter. A study conducted on Weddell seals at the Vestfold Hills (Prydz Bay) suggested that the seals exploit areas where environmental forces crack the fast ice providing access for breathing and hauling out (Lake *et al.* 2005). Cracks are likely to form in direct association with land or other obstacles that limit ice movement under atmospheric or oceanic forcing. The coastal area off Adélie land is characterized by the presence of several islands and a glacier that could facilitate crack formation in the sea-ice. Previous studies on Weddell seals revealed large individual variations in their use of the winter ice environment, with some animals moving between pack ice where they fed, to fast-ice where they hauled out (Testa 1994b; Lake *et al.* 2005, 2006). Our models did not reveal any significant effect of sea-ice concentration on Weddell seal diving behaviour. This is probably a result of the mismatch between the coarse resolution of sea-ice concentration data (≈ 36 km^2 cell grid) and the relatively limited geographical scale of the seal movements (average distance from the colony 34 km) which encompassed relatively low variation in sea ice concentrations.

5.2.2 Bathymetry

Weddell seals as other predators are likely to select foraging areas associated with predictable prey distribution and with physical features that allow a better accessibility to the prey (Burns & Kooyman 2001; Watanabe *et al.* 2003; Burns *et al.* 2004). Foraging in shallow coastal waters as observed in Dumont D'Urville seals may give access to prey located at short vertical distances from surface and aggregated in patches near the seafloor that would be more easily caught than in deeper waters (Burns *et al.* 2004, 2008). Furthermore, Weddell seals have been observed in shallow waters of the Ross sea pursuing pelagic fish from the midwater down to the sea bottom where prey were trapped on the seafloor (Fuiman *et al.* 2002). Both strategies may have been used by seals from Dumont D'Urville as suggested by their preferential usage of shallow waters instead of the deep waters of the D'Urville Trough also available at similar distance from the colony.

Weddell seals of Dumont D'Urville increased the time spent at the bottom of the dives when the seafloor was smoother, suggesting that they could allocate more time hunting for prey when bathymetric obstacles on the seafloor were limited. This may be particularly important for Weddell seals foraging in thick sea-ice such as Dumont D'Urville seals, as a significant part of their dive time is used for horizontal travel underneath the sea-ice to access their breathing holes (Watanabe *et al.* 2003; Mitani *et al.* 2004).

5.2.3 Hydrology

Weddell seals used MCDW throughout the study period, and predominantly during winter. In late summer/autumn, AASW and AASW/MCDW were also used. The coastal area off Adélie Land is associated with a complex bathymetry which influences the hydrological regimes of the area. Bathymetric features could induce upwelling of a

macronutrient enriched water mass, the Circumpolar Deep Water (CDW) flowing southward over the continental Antarctic shelf from the Antarctic Circumpolar Current (ACC) (Tynan 1998; Prézelin *et al.* 2000). Whilst upwelling toward the coast, the CDW becomes modified by contact with the AASW to form the MCDW (Williams *et al.* 2010; Lacarra *et al.* 2011). A recent hydrographical analysis of the D'Urville Trough revealed the presence of MCDW from the northern part of the trough to the coastal edges suggesting a flow of this water mass from the d'Urville Trough to the coastal zone and the Adélie Bank (Lacarra *et al.* 2011). Previous studies showed correlation between reproductive krill and areas influenced by the CDW (Prézelin *et al.* 2000; Nicol 2006). Indeed, intrusions of the relatively warm CDW on the continental shelf provide high concentrations of nutrients to AASW that stimulates phytoplankton growth (Sievers & Nowlin 1984). This could increase regional primary production and enhance secondary production (Tynan 1998; Prézelin *et al.* 2000; Ducklow *et al.* 2007), hence improved feeding conditions for top predators. In addition, intrusion of warmer CDW, accelerates embryonic development and provides a transport path for krill larvae from deep water to the continental shelf (Hofmann *et al.* 1992; Hofmann & Hüsrevoğlu 2003). Larvae of *P. antarcticum* are thought to spawn in deep coastal canyons or in coastal zones near ice-shelves or glaciers (Koubbi *et al.* 2009) and juveniles of *P. antarcticum* are mostly found in association with MCDW intrusions onto the continental shelf (La Mesa *et al.* 2010). The presence of a deep canyon and the prevalence of MCDW in the coastal area off Adélie Land could therefore result in particular assemblages of species including *P. antarcticum*, making this region a profitable area for Weddell seals.

5.3 Future studies

Direct information on prey distribution in the Southern ocean remains very scarce and without a direct measure of feeding events, monitoring the foraging success of marine predators remains a difficult task. For Weddell seals, the bottom phase of dives has been shown to be associated with significantly higher prey availability than the descent and ascent phase (Watanabe *et al.* 2003; Mitani *et al.* 2004). Maximum dive depth thus provides information both on the part of the water column targeted by the seals and on their prey distribution and Rbt could be considered as a measure of foraging effort (see methods section 2.6). Theoretical studies on foraging behavior often assume that the number of prey encountered increases with time spent searching (Kramer 1988; Houston & Carbone 1992). However, an increased searching effort can reflect the scarcity of prey and therefore not indicate necessarily feeding success (Bailleul *et al.* 2008). Drawing conclusion on the foraging success of Weddell seals during winter is therefore difficult and further studies should integrate instrumentation from which it could be inferred (Davis *et al.* 2003; Naito *et al.* 2010).

Our understanding of Weddell seals habitat use during winter could also be improved by using some of our environmental data at a more appropriate scale. In absence of direct ambient light measurement we used sun position as a proxy for light intensity. However, sun position doesn't take into account sea ice or weather conditions, which are likely to influence the actual light intensity available for seals and potential prey in the water column. Using light sensors would help identify more precisely the effect on light intensity on feeding behaviour. Further work could also investigate how individual seals exploit holes and cracks in the fast ice using sea ice data with a higher spatial resolution such as MODIS satellite imagery (Massom *et al.* 2009).

6. Conclusion

This first study on movement patterns and foraging behaviour of Weddell seals in Adélie Land has shown that seals reside within coastal areas throughout winter. Weddell seal behaviour was significantly related to bathymetric features and water mass type, but not with ice concentration at the spatial resolution used in this study. Seals are likely to optimize their foraging strategies to face harsh winter conditions (increase in ice cover, reduced light intensity) by making more exploratory dives, possibly to find prey patches occurring at low density during winter. They appeared to track the diel migration of their prey and targeted shallow waters with a smooth bathymetry that may increase prey accessibility. The water mass composition of the water column influenced diving behaviour as individuals increased their foraging effort in AASW, while MCDW was targeted preferentially during winter. In order to determine whether finer scale parameters improve our models, future work will consider vertical features of the water column and incorporate higher resolution sea ice distribution data.

7. Ackowledgement

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8. Appendix

S4.1 Extraction of environmental information: an example for sea ice concentration

Sea ice concentration was extracted from AMSR-E sea ice concentration images (http://www.iup.unibremen.de:8084/amsredata/asi_daygrid_swath/l1a/s6250/). Each "pixel" in the image has an allocated ice concentration and is equal to 5.95km X 6.57km. Ice concentrations were extracted at each Argos, Kalman smoothed and GPS location using the R package (R Development Core Team; library sp, function overlay).

In addition, at each Kalman smoothed location, a weighted mean of ice concentration [ice] was extracted by weighting each point in the AMSR-E position by the associated error ellipse from the Kalman filter. Therefore, the weighted ice concentration is given by:

$$\overline{[ice]} = \frac{\sum_{i=1}^{n} w_i [ice_i]}{\sum_{i=1}^{n} w_i}$$

where the wi are weights are given by

$$w_i = \frac{1}{(2\pi)|\Sigma_i|^{1/2}} e^{-\frac{1}{2}(\mathbf{x}_j - \mu_i)^T \Sigma^{-1} (\mathbf{x}_j - \mu_i)}$$

which is the probability density function for a bivariate Gaussian probability density function. Here $\mathbf{x}_j$ is the jth grid-coordinate {x-coordinate, y-coordinate} where the ice concentration, μ_i is the point estimate (expected) location from the Kalman filter and Σ_j is the estimated variance-covariance matrix from the Kalman filter for the ith location. The same method was used to calculate a weighted mean of the bathymetry at each dive location.

Table S4.1. Results for the most parsimonious generalized mixed-effects models relating Weddell seal diving behaviour to their environment (see Table 3 for model terms definition). Term coefficients are presented ± SE and p-values for each coefficient are also shown. Significant terms ($P < 0.05$) are denoted by bold characters. For YR, DN, and WM variables that were coded as factors in the model, coefficients are given in reference to 2007, Day, and AASW.

Environmental variables	Dive response variables					
	Maximum dive depth (DEP)		Duration (DUR)		Residual bottom time (Rbt)	
	Coefficient ± SE	**Coefficient P**	**Coefficient ± SE**	**Coefficient P**	**Coefficient ± SE**	**Coefficient P**
Bathymetry (BAT)	**0.25 ± 0.01**	**< 0.0001**	**29.86 ± 7.31**	**< 0.0001**	**-**	**-**
Slope (SLP)	**- 0.05 ± 0.01**	**< 0.0001**	**-**	**-**	**- 3.69 ± 1.17**	**< 0.01**
Day of Year (DOY)	**- 0.001 ± 0.0002**	**< 0.01**	**0.52 ± 0.11**	**< 0.0001**	**-**	**-**
Year (factor) (YR)	**-**	**-**	**-**	**-**	**-**	**-**
Night (factor) (DN)	**- 0.35 ± 0.02**	**< 0.0001**	**- 124.79 ± 11.80**	**< 0.0001**	**- 20.79 ± 5.53**	**< 0.001**
Twilight (factor) (DN)	**- 0.14 ± 0.02**	**< 0.0001**	**- 37.86 ± 12.48**	**< 0.01**	**- 16.66 ± 5.91**	**< 0.01**
AASW/MCDW	0.07 ± 0.05	0.21	18 ± 31	0.56	**-61.26 ± 14.88**	**< 0.0001**
MCDW	**0.18 ± 0.05**	**< 0.001**	-11.92 ± 28.65	0.68	**-70.14 ± 13.13**	**< 0.0001**
MSW	**0.21 ± 0.05**	**< 0.001**	-15.73 ± 32.48	0.62	**-71.78 ± 14**	**< 0.0001**
LSSW	0.08 ± 0.0	0.17	29.91 ± 31.42	0.39	**-85.38 ± 14**	**< 0.0001**
HSSW	**0.17 ± 0.07**	**< 0.01**	38.70 ± 37.61	0.30	**-84.32 ± 16.64**	**< 0.0001**
ISW	**0.21 ± 0.09**	**< 0.05**	**135.65**	**< 0.01**	**-92.96 ± 24.29**	**< 0.0001**

C - Paper 5

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Where to Forage? Contrasting behaviour between two colonies of Weddell seals in East Antarctica

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1. Abstract

Winter is a critical period in the Weddell seal life cycle when seals must optimize their resource acquisition and storage to maximise breeding success in spring. However, Weddell seals' interaction with their winter environment remains poorly documented. We equipped adult Weddell seals with satellite relayed data loggers at two sites in East Antarctica: Dumont D'Urville (n = 12, DDU) and Davis (n = 20). The tags transmitted Argos positions and dive information from DDU seals over 183 ± 13 days (30319 dives) and from Davis seals over 158 ± 7 days (50170 dives). Intensive foraging activity (*i.e.* "hunting" mode) was detected using a tracked-based method that integrates a vertical index that quantifies time spent foraging within each dive (*i.e.* hunting time), thereby integrating the horizontal, vertical and temporal dimensions simultaneously. Environmental variables (*i.e.* bathymetry, slope, sea-ice) were extracted for each location by taking mean values from 100 simulated tracks to account for Argos positioning errors. We used binomial generalized mixed effect models (GLMM) to investigate Weddell seals' behavioural response (*i.e.* "hunting" vs "transit") to their environment. The optimal Area Restricted Search spatial scale (4-5 km) suggested Weddell seals intensified their hunting behaviour around a given access-hole in the ice until resources have depleted. Moreover, Weddell seals from the two different sites exhibited different foraging strategies: hunting dives were relatively restricted to specific areas at DDU; while more dispersed at Davis. However, hunting dives recorded at both locations were mostly pelagic and in highly concentrated ice above shallow bathymetry surrounded by canyons and depressions. The switch toward hunting behaviour was influenced by some key environmental features, including the bathymetry, sea-ice derived metrics (*i.e.* distance to ice edge, spatial variability of sea-ice) and the advance of winter (which was particularly important). Weddell seals exhibited behavioural plasticity in contrasting environments, suggesting habitat selection was associated with predictable prey availability and accessibility. Our study highlights the

difficulty in predicting Weddell seals' habitat use, but demonstrates the utility of our newly-developed foraging metric at the small scale (< 1km).

Keywords: Pinnipeds, movement patterns, winter, first passage time, habitat use

2. Introduction

In the marine environment, resources are heterogeneously distributed both in time and space. This heterogeneity is driven by physical structures at different scales in the environment. In order to maximize prey acquisition predators are expected to concentrate their search behaviour in areas associated with higher prey density (Fauchald & Tveraa 2003). In the case of marine predators, for which prey capture occurs at depth, this could be achieved by decreasing its displacement speed and increasing the sinuosity of its track both in the horizontal and vertical dimensions (Kareiva & Odell 1987). The detection of these behavioural switches (*i.e.* area restricted search, ARS) and the associated environmental features is crucial to understanding predators' fitness and survival.

In winter, Antarctic predators face increased sea-ice cover and modified hydrological regimes, as well as lower marine productivity due to limited sunlight (Burns *et al.* 2004; Bailleul *et al.* 2007; Meiners *et al.* 2012). The Antarctic shelf appears to be of crucial importance for several species foraging during Antarctic winter (Burns *et al.* 2004; Chapman *et al.* 2004; Bailleul *et al.* 2007; Ribic *et al.* 2008). The shelf itself is associated with a complex bathymetry including underwater canyons, seamounts, banks and troughs (Ribic *et al.* 2008). Interplay between these bathymetric features and other physical components such as the hydrological circulation are likely to influence prey distribution and availability on the shelf (Chapman *et al.* 2004; Nicol *et al.* 2010; Heerah *et al.* 2012). The sea-ice environment is a particular key habitat of the shelf and favoured by multiple marine predator species during winter (southern elephant seals: (Muelbert *et al.* 2013), crabeater seals: (Burns *et al.* 2004, 2008), emperor penguins [*Aptenodytes forsteri*]: (Rodary *et al.* 2000), Weddell seals [*Leptonychotes weddellii*]: (Heerah *et al.* 2012)). Indeed, sea-ice serves as a substrate for sea-ice algae (which is the basis of the trophic food

web in turn used by predators) and a refuge from other predators. Sea ice also represents a physical barrier, constraining the movements of air-breathing animals and their access to favourable foraging grounds (Tynan *et al.* 2009). In winter, the presence of polynyas in fast-ice areas can influence air-breathing predators' distribution as they offer access to open water and potentially easier prey accessibility (Tynan *et al.* 2009; Massom & Stammerjohn 2010).

East-Antarctica is defined as the region of the Indian and Pacific sectors between 80 and 160°E. It encompasses the CCAMLR (the Commission for the Conservation of Antarctic Marine Living Resources) division 58.4.1 and is a source of Antarctic bottom water (*e.g.* Adélie land) showing its importance from both an ecological and an oceanographic perspective (Nicol *et al.* 2010). A biological/oceanographic survey conducted eastward from Davis (68°58'S 77°97'E) to Dumont D'Urville (DDU) (66°40'S 140°E) observed major differences in the physical and biological environment between the eastern and western sections of the survey area (Nicol *et al.* 2010). Nicol *et al.* (2010), showed that productivity at all levels (*e.g.* primary productivity, zooplankton, whales and seabirds) was influenced and delimited by the southern boundary of the Antarctic Circumpolar Current (ACC). For instance, productivity occurs in a wider band where the southern boundary of the ACC is located further offshore (*i.e.* western section of survey area [80-115°E] close to Davis), whereas productivity is concentrated nearer to the coast as the southern boundary of the ACC approaches the coast (115-150°E encompassing DDU). Sea ice conditions are also markedly different between Davis and DDU. The seaward extent of permanent fast-ice (6-10 km extent) surrounding the Vestfold Hills at Davis is relatively less than other locations (45-65 km extent) in East Antarctica (Fedotov *et al.* 1998). The Vestfold Hills area is also characterized by a large coastal polynya estimated to be eight times the size of the Mertz glacier polynya (138-148°E)

persistingnearby DDU (Arrigo & Van Dijken 2003). The Antarctic shelf offshore from the DDU site is characterized by the deep d'Urville trough which extends from the coast at 141°E to the northwest, and the shallow Adélie bank (Beaman *et al.* 2011). Davis is located in a bay (*i.e.* Prydz bay), which is characterized by a broad basin (*i.e* Amery depression) and two elongated deep channels. One of these channel is parallel to the Davis coastline; the other is located further offshore on the edge of the Amery depression (O'brien & Leitchenkov 1997).

The Weddell seal represents an ideal candidate to study Antarctic-shelf habitat use during winter because it is the only Antarctic air-breathing marine predator adapted to breathe through holes in continuous ice cover (Kooyman 1981). It is the second deepest Antarctic phocid diver (after the southern elephant seals *Mirounga leonina*), diving more than 900 meters in East Antarctica (Heerah *et al.* 2012), and capable of holding its breath longer than other comparably sized species (Kooyman 1981; Tynan *et al.* 2009). These physiological adaptations enable them to access the under-ice habitat across several kilometres and to forage on a range of species at depth such as fish, cephalopods and crustaceans depending on the age, the season and the location (Kooyman 1981; Burns *et al.* 1998; Lake *et al.* 2003; Ainley & Siniff 2009b). These movement characteristics are of particular importance to maximize prey acquisition during the Antarctic winter when productivity is reduced (Meiners *et al.* 2012). Their movements and haul-out sites have been studied in several Antarctic locations during winter, such as the Ross sea (Testa 1994b; Burns *et al.* 1999; Burns & Kooyman 2001) and Prydz bay (Lake *et al.* 2005, 2006; Andrews-Goff *et al.* 2010). However, only one study to date have assessed their behavioural response to the Antarctic winter environmental conditions (Heerah *et al.* 2012). Moreover, the definition of Weddell seal's habitat utilization, based on existing track-based methods (*e.g.* state space models, first-passage time) is challenging because of their small

scale, highly sinuous and sea-ice constrained movements which could be misleading in ARS identification. In the present study, we overcome this limitation by defining ARS according to Weddell seals' diving behaviour by integrating a vertical foraging metric into a customized track-based method.

Ours is the first study comparing the winter foraging behaviour of two Weddell seal populations. Using a new approach that integrates Weddell seal movements in the 3D our study aimed to answer two main questions: (i) what are the foraging strategies adopted by Weddell seals in contrasting environments? (ii) which environmental parameters (*i.e.* bathymetry, slope, sea-ice, distance to open water, spatial ice variability) are likely to influence their behaviour? We expected the seals to favour open water areas within the fast-ice or areas associated with perennial tidal cracks that facilitate access to the surface (Siniff *et al.* 2008). We also expected seals to principally use shallow coastal areas (as observed in Lake *et al.* 2005; Heerah *et al.* 2012) in association with bathymetric features (*e.g.* canyons, depressions) likely to influence hydrological regimes, and consequently, prey availability (Tynan 1998; Prézelin *et al.* 2000).

3. Material and methods

3.1 Instrumentation

The study was conducted at two sites of East Antarctica: Dumont D'Urville (DDU) (66°40'S 140°E) and Davis (68°58'S 77°97'E), during three winters for each site (DDU: 2007-09, Davis: 2006-07 and 2011). Adult Weddell seals were captured after their annual moult in February at DDU (Nfemale = 9 and Nmale = 3, length: 230 ± 3 cm and mass: 284 ± 17 kg) and in March-April, depending on the year, at Davis (Nfemale = 18, Nmale = 2, length: 240 ± 3 cm and mass: 365 ± 13) (Table S5.1). Similar capture and tagging procedures were used at both sites and are fully described in (Heerah *et al.* 2012). Satellite relayed data loggers (SRDLs) were head mounted on the Weddell seals, recording their displacements and diving behaviour for the whole winter. Seals (n = 9) for which the tag did not transmit for longer than 90 days were removed from the dataset.

3.2 Argos locations filtering and track simulations

The accuracy of an Argos location depends on the duration and number of uplinks between satellites and the SRDL. Argos locations are provided with a location class (LC) that estimates the radius of uncertainty associated with each location (Service Argos, 2010). These radii encompass the 68^{th} percentiles predictions (separately for latitude and longitude) rather than the full error (Costa *et al.* 2010). In our dataset, 42 % of the locations were associated with an estimated error ranging from 250 m to 1500 m (classes from 3 to 0), 42 % had no accuracy estimation (classes A and B) and 5 % (class Z) were invalid and therefore removed from the dataset. Studies on free-ranging animals reported larger errors than those indicated by Argos (Costa *et al.* 2010; Silva *et al.* 2014) and our dataset was acquired before the integration of a Kalman filter into the Argos algorithm to estimate

positions (Silva *et al.* 2014). Consequently, we filtered the Argos locations using a combination of: (i) a swim speed filter with the maximum speed set to 20 $km.h^{-1}$, which resulted in the removal of 15 % of the Argos locations and (ii) a Kalman filter that accounted for location error according to their assigned Argos LC (R package "crawl"; Johnson 2013). Briefly, this algorithm uses a correlated random walk model (CRWM) to predict the next position and its estimated error based on the previous positions and estimated error (Johnson *et al.* 2008). The continuous-time formulation allows the data to be used without being sub-sampled or aggregated to fit into a regularly spaced time-scale. This enables small scale movements to be retained which is of particular importance when considering the movement ranges of Weddell seals from DDU and Davis (see Table S5.1, (Johnson *et al.* 2008)). We then fitted CRWMs to our Argos locations to predict a location and estimated error for each dive according to its time (Johnson *et al.* 2008). Finally, to account for location error when extracting environmental variables, we used the fitted CRWM to create a dataset of 100 simulations of each dive location (Fig. S5.1, (Johnson *et al.* 2008)). These steps were performed for each individual seal.

3.3. Environmental data

We used two bathymetric datasets according to their spatial coverage. A fine-scale bathymetry dataset (Beaman *et al.* 2011, 100 m cell grid resolution) was merged with locations from 10 seals (out of 12) from DDU that did not travel west of 138°E, which was the longitudinal limit of this data set (http://data.aad.gov.au/). Broader-scale GEBCO bathymetry (30 sec [~1 km] cell grid resolution) was merged with seal locations from Davis and the two individuals from DDU that travelled west of 138°E (http://www.gebco.net/). The bathymetric slope (hereafter "slope") was calculated for each grid cell from the bathymetry values of the eight neighbouring cells using the R software package *raster* (R

Development Core Team 2008; function *terrain*; (Hijmans 2014)). We also calculated the distance between each dive and the nearest coastline (closest positive bathymetry value, *i.e.* land). The bathymetry and its slope were extracted for each dive location taken from the 100 simulated tracks to account for Argos location errors for each dive using the R package *raster* (R Development Core Team 2008; function *extract*; (Hijmans 2014)). Finally, the 100 bathymetry and slope values associated with each possible dive location were averaged, giving a mean value and its standard deviation for each location along the main track.

Sea-ice concentration was sourced from AMSR-E daily sea-ice concentration images (http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html). Each "pixel" in the image (5.95 km x 6.57 km) had an ice concentration value (ranging from 0 to 100 %). Sea-ice concentration values were extracted for each dive following the same procedure outlined by the bathymetry and slope extraction method above. Two other variables were calculated using the sea-ice concentration data: (i) the distance to the closest area of ice concentrations below 20 % (hereafter "distance to ice edge") instead of the 15 % threshold commonly used because DDU and Davis are located in coastal fast-ice areas (M. Vancopenolle, pers. com.) and; (ii) an index of the spatial variation of sea-ice concentration in the vicinity of each dive. The latter was calculated as the standard deviation of sea-ice concentrations within a radius of 25 km around each dive (hereafter "sdice25").

In a previous study, Heerah *et al.* (2012) found that light intensity associated with the time of day influenced Weddell seals' diving behaviour. Consequently, the period of the day associated with each dive was considered. The R package *maptools* (R Development Core Team 2008; function *solarpos;* Bivand & Lewin-Koh 2014) was used to calculate sun angle above or below the horizon for each dive according to local time and we then divided days into three periods: day (sun above horizon), twilight (sun between 0 and 12 ° below horizon), night (sun > 12° below horizon).

3.4 Diving behaviour

3.4.1 Data collected from the tags

The SRDLs were programmed to record dive depth and time every four seconds. From these records, the start and end time of each dive, dive duration, maximal depth and post-dive surface interval were determined. Uplinks were attempted every 40 seconds when the seal surfaced and data were transmitted for a random subset of dives (drawn from memory). The four main inflexion time-depth points where the dive shape changed most rapidly were also transmitted (see (Fedak *et al.* 2002) for details on dive profile summarizing procedure). This provided a total of 144107 dive profiles for the 32 focal Weddell seals. However, rounding errors resulted in several null dive durations or total dive durations shorter than the time since the last time inflexion point, similar times in successive depth points, artificially long dives that were obviously two dives instead of one, and artificially deep dives (> 1500 m) with unrealistic shapes. These dives were removed from our dataset (~33 % of the dives). Dives below 20 meters represented 5 % of the total time spent diving and were also removed from our dataset (~12 % of the dives).

For each dive we also calculated the difference between the maximum dive depth and corresponding bathymetry (hereafter "depth difference"). We found that 26 % of maximum dive depths were greater than the bathymetry, likely due to the combined error of both bathymetry and seal positions. The depth difference was normally distributed with a mode between -30 and 30 m for dives from DDU and a mode between -50 and 50 m for dives from Davis, suggesting that these modes represent dive to the sea-floor (*i.e.* benthic dives) (Heerah *et al.* 2012). This suggests that dives 30 m and 50 m deeper than the bathymetry (hereafter "error threshold") in DDU and Davis respectively are likely due to bathymetry and/or seal position error. Consequently, these dives were removed from the dataset (DDU: 5 % of the dives, Davis: 8 % of the dives). Dives associated with a positive bathymetry value (*i.e.* land) was likely due to dive position error and were also removed from the dataset (4 % of the dives). Dives were then separated into two types: (i) benthic

dives (*i.e.* maximum dive depths within the error threshold); and (ii) pelagic dives (*i.e.* with maximum dive depths shallower than the error threshold).

3.4.3 Calculation of a vertical foraging metric: the hunting time

Heerah *et al.* (2014) developed a method to detect the intensification of foraging effort within a dive using either high- or low-resolution time-depth data (see also Part I Paper 3 of the thesis). This method assumes that a seal increases its time spent in a prey patch by increasing the vertical sinuosity of its path and decreasing its vertical velocity – effectively Area Restricted Search (ARS) in the vertical rather than the horizontal plane. For southern elephant seals (*Mirounga leonina*), prey capture attempts (inferred from high-resolution acceleration data) mostly (77%) occurred in highly sinuous parts of the dive, independently defined as "hunting" phases (versus less sinuous parts defined as "transit" phases). Because it is not possible to calculate vertical sinuosity using low-resolution dive profiles (*i.e.* acquired from SRDLs), we (see Part I Paper 3) investigated the correlation between the time spent "hunting" within a dive (estimated from vertical sinuosity) and several potential low-resolution foraging indexes. The highest correlation was found with time spent in low-resolution dive segments associated with reduced vertical rates of change. Moreover, dive segments with low vertical rates of change were also highly associated with prey capture attempts (71%) identified by accelerometers. The SES dataset allowed to validate the method that was similarly applied to Weddell seal dives.

Thus, for each of the five segments from each dive (*i.e.* as provided by SRDLs), we calculated the concurrent vertical rate of change (*i.e.* vertical velocity, $m.s^{-1}$). Segments with vertical velocity ≤ 0.2 $m.s^{-1}$ were defined as "hunting" segments, whereas segments with vertical velocity > 0.2 $m.s^{-1}$ were defined as "transit" segments (see Part I paper 3). The total time spent in the "hunting" segments within a dive was used as a vertical foraging effort metric in further analysis (Heerah *et al.* 2014).

3.5. Movement pattern analyses

We used two track-based methods to identify behavioural switches along a seal's path: (i) first-passage time (FPT) and (ii) an alternative of the FPT method that integrated the vertical component of foraging activity (*i.e.* hunting time) termed here first-hunting time (FHT).

3.5.1 First-passage analysis

First-passage time measures the time an animal takes to cross a virtual circle of radius *r* that is moved along its track (Fauchald & Tveraa 2003). First-passage time increases with increasing radius but this increase will be particularly large when individuals significantly change their behaviour (*i.e.* switch between transit and ARS behaviour). Thus, by plotting the variance in FPT against a range of radii tested it is possible to identify the spatial scale at which search effort is concentrated (Fauchald & Tveraa 2003). In this study, the FPT analysis was performed using a customized R algorithm (available upon request to the authors). A circle of radius *r* was centred on each filtered dive location and the time elapsed between the first and the last successive dives within that circle were measured. This step was repeated for each dive along a seal's path, thus providing an index that estimates the FPT for each dive. The procedure was repeated for radii from 500 m to 15 km; increasing by 100 m increments between 500 m and 1 km, by 200 m increments between 1.2 km and 5 km, and by 500 m increments between 5.5 km and 15 km. Radii were chosen to reflect the small scale movements of Weddell seals and to be ecologically meaningful for this species (*e.g.* sea-ice concentration is expected to constrain seal habitat selection as they rely on ice-holes to breath). The minimum radius size was not less than 500 m because only 25 % of dive locations were associated with estimated error lower than 500 m. The spatial scale of concentrated search effort was defined, for each seal, as the mean peak in log-transformed variance in FPT (to make the variance independent of the magnitude) relative to radius size (see results and Fig. 5.4). We chose to retain the optimal

spatial scale for each seal instead of averaging them among all individuals, as their range of displacements varied dramatically from one another (see results and Table S5.2).

3.5.2 Integration of a vertical foraging metric: the first-hunting time analysis

It has been reported that FPT analysis correlates well with inferred foraging success in pinnipeds (Thums *et al.* 2011; Dragon *et al.* 2012b). However, Bailleul *et al.* (2008) showed that a method which integrates diving behaviour with horizontal displacement improved the overlap between foraging success and search areas. We therefore adapted the FPT method by integrating the time spent hunting within each dive (*i.e* hunting time, see above and Part I Paper 3 for a full description of the index). This method adopts the same procedures used in FPT analysis described above, except that instead of measuring the time required to cross a circle of given radius, it sums the total time spent hunting within that circle. This adaptation allowed us to identify behavioural switches at depth (at the optimal spatial scale for each individual) and is termed the first-hunting time (FHT). (Fauchald & Tveraa 2003) defined search areas as the areas associated with the longest FPT. Similar to (Thums *et al.* 2011), we used the distribution of FHT density estimates to find a time threshold discriminating the mode of lower FHT values (*i.e.* "transit") from all other higher modes (*i.e.* "hunting"). A simple algorithm was used to find this time threshold automatically for each individual. First, it identifies the FHT value corresponding to the first maximum of the density estimates curve (*i.e.* lower FHT values mode Fig. S5.2 a): $FHTdens_{max}$. Second, it calculates the derivative of the density estimates curve (Fig. S5.2 b). Finally, it finds the FHT value associated with the first minimum of the derivative occurring after $FHTdens_{max,}$ which corresponds to the inflexion point of the lower FHT value mode (see Fig. S5.2 a-b). Dives with FHT values below the time threshold were defined as "transit" dives, whereas dives with FHT values above the time threshold were considered "hunting" dives. We then plotted daily FHT at the optimal spatial scale for each individual and dives associated with intensified hunting at depth (Fig. S5.2 c-d).

3.6 Statistical analysis

We fitted a series of generalized mixed effect models (GLMM) with multivariate normal random effects, using penalized quasi-likelihood (R package "MASS", function "glmmPQL", Venables and Ripley 2002) to examine the relationship between our binary behavioural response variable ("transit" vs "hunting" dives) and the explanatory variables (*i.e.* temporal [year, day of year], site, and environmental factors [bathymetry, slope, distance to ice edge, *sdice25*]). We used this type of GLMM instead of the one more commonly used (*i.e.* provided by the R package "lme4", Bates et al 2014; *e.g.* (Muelbert *et al.* 2013; O'Toole *et al.* 2014) because it enables the addition of an auto-correlation term to avoid violation of the "independence" assumption when dealing with time series dataset (*e.g.* tracking data, dive series, environmental time series) (Zuur *et al.* 2009, 2010)(Zuur et al. 2009 a and b). Thus, an autoregressive variance-covariance matrix (cor AR1 in R, R development core team 2009), representing first-order autocorrelation structure, was added to model the serial correlation among observations (Zuur et al. 2009a). Individual seal was included as random term on the intercept to take into account inter-individual variability (Zuur et al. 2009a). Missing and outlier values were removed from the dataset prior to analyses. Thus, 58090 dives (73% of the remaining dives, see method section 3.4.1) and their concurrent environmental values were retained for further analysis. Non-collinearity was verified between continuous variables using Pearson correlation (coef < 0.5) and the variance inflection factor (VIF) (Zuur *et al.* 2010). All explanatory variables were standardized (centred and scaled) to facilitate model convergence and enable comparison of their respective contribution (using their corresponding slope coefficients). Because we used "glmmPQL", model selection can only be performed according to p-values and model residuals output.

We ran three sets of models: one which considered dives from both locations (set 1) and the other two only considered dives from one location (either DDU: set 2 or Davis: set 3). Due to computational limitations, models from set 1 and 3 were performed using a

random sub-sample of dives (1/3 dives for set 1 and 1/2 dives for set 3). For each set we started with a full model that included all environmental variables and meaningful variable interactions (*e.g.* influence of site [set 1] and year within site [set 2 and 3]). We then implemented a stepwise procedure to remove non-significant variables with the threshold set at p-value < 0.05 (Zuur *et al.* 2009). Finally, GLMMs were validated by examining the residuals distribution (*i.e.* normal distribution, verification of normality) and checking for any potential trend between residuals and each explanatory variable (*i.e.* verification of homogeneity) (Zuur *et al.* 2009).

Wilcoxon rank-sum tests were used to compare average movement, behavioural and environmental metrics between (i) sites, (ii) behavioural modes (*i.e.* hunting and transit) within each site and (iii) each behavioural mode between sites (see results and Table S5.1-S5.4). The Wilcoxon rank-sum test is adapted for comparing two samples of a two levels factor when data do not have a gaussian distribution and is considered more conservative if data are normally distributed (Crawley 2012). Samples were constituted of the means of the metric of interest for each individual separately and were therefore independent.

4. Results

4.1 Tag performance

Over the six-year study, the winter trips greater than 90 days of adult female Weddell seals from DDU (n=12) and Davis (n=20) were tracked for 183 ± 13 days (mean ± SE, max: 242 days) and 158 ± 7 days (max: 199 days) respectively, from late February to mid-October (Table S5.1, Fig.5.1). Most tag data were collected from March to August with 20 individual tracks being recorded over this entire period (Table S5.1, Fig.5.1). After preparation of the dataset (see Materiel and methods), a total of 30319 dives (15 ± 0.9 dives per day, max: 82) were available for analysis for seals from DDU and 50170 dives (18 ± 0.9 dives per day, max: 81) for seals from Davis (Table S5.1).

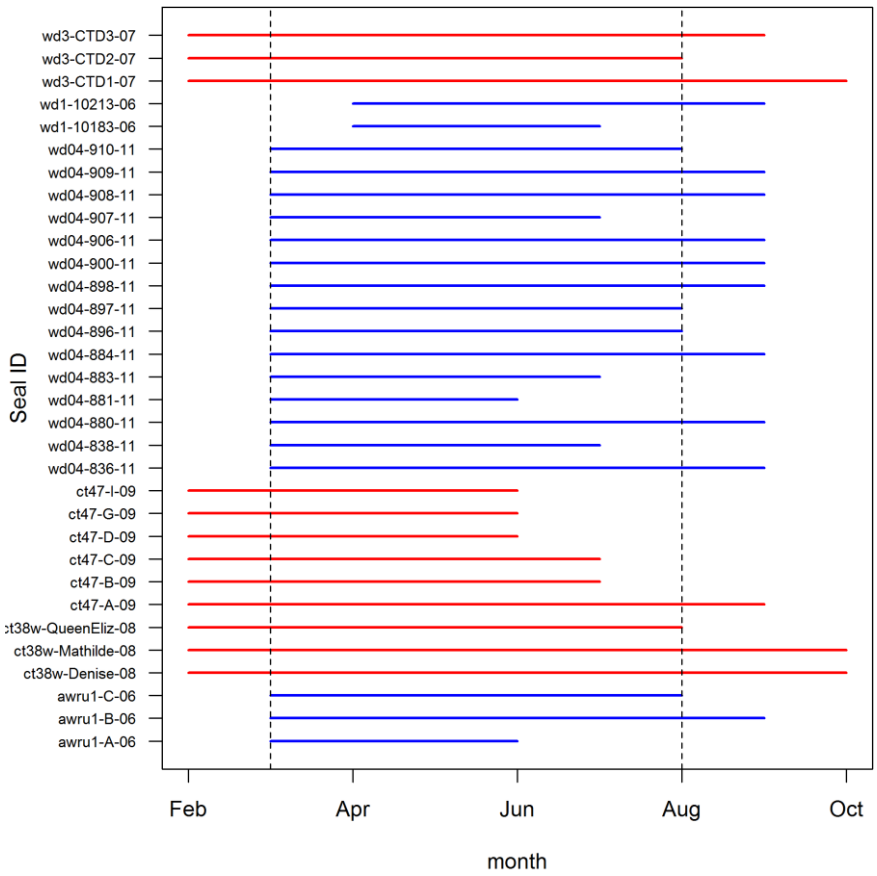

Figure 5.1. Temporal coverage of each individual dataset from DDU (blue lines) and Davis (Red lines). Dotted vertical lines represent the period when most data was collected.

4.2 Movement patterns

Overall, seals from both sites had a coastal distribution and remained on the Antarctic continental shelf (Fig.5.2). However, there were marked differences in the scale movements among individuals within each site and between the two sites.

For each seal from DDU the mean distance from the shoreline and deployment site ranged from 1 ± 0.03 km to 25 ± 0.3 km (max: 78 km) and from 2 ± 0.05 km to 74 ± 1 km (max: 259 km) respectively (Table S5.1). On average, these seals travelled 4 ± 1 km day^{-1} (max: 75 km day^{-1}), although average distances for each seal ranged from 0.5 ± 0.04 $km.day^{-1}$ to 12 ± 1 $km.day^{-1}$ (Table S5.1). Most seals remained in the vicinity of the site, however, three individuals travelled beyond this zone: one to the D'Urville Trough (wd3-CTD3-07), one to the western (ct47-B-09) and one to the eastern (ct47-D-09) parts of the shelf in the study area (Fig.5.2 a).

In contrast, seals from Davis travelled, on average, distances that were three times larger than the ones covered by the seals in DDU (p-values < 0.05, see Table S5.1). Average travel distances covered by individuals from Davis ranged from 4 ± 0.05 km to 116 ± 1 km (max: 293 km) from the coast and 18 ± 0.1 km to 169 ± 1 km (max: 372 km) from the deployment site (Table S5.1). Overall, seals travelled 11 ± 1 $km.day^{-1}$ (max: 144 $km.day^{-1}$), although average distances for each seal ranged from 3 ± 0.3 $km.day^{-1}$ to 21 ± 2 $km.day^{-1}$. Most seals from the Davis site travelled to the north-eastern part of the shelf while five others travelled west to the middle shelf area but only one travelled north (wd4-880-11), diving over the shelf break and in areas deeper than 2000 m (Fig.5.2 b).

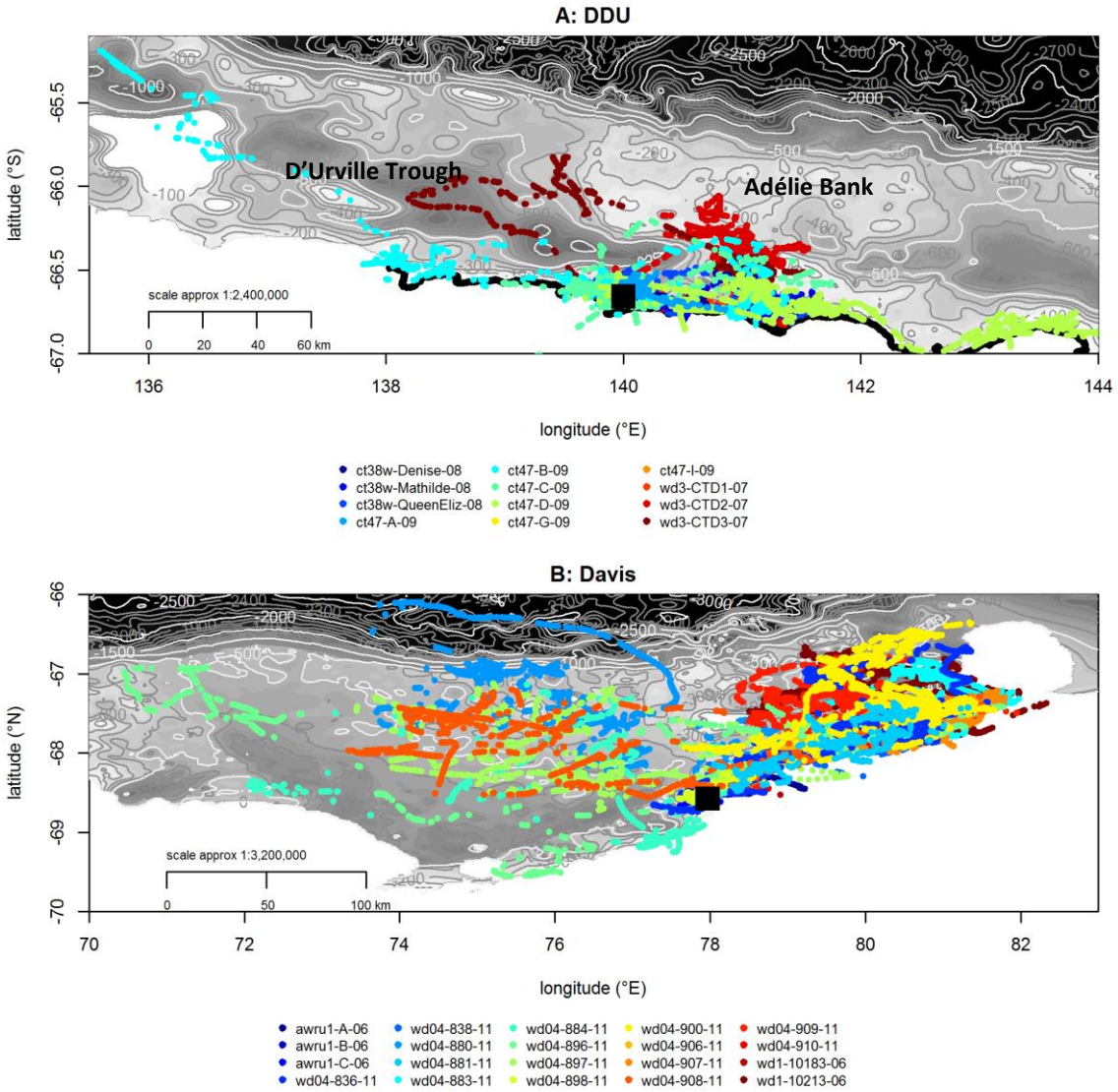

Figure 5.2. Tracks of SRDL equipped Weddell seals from Dumont d'Urville (A) and Davis (B) during 2007-09 and 2006-07/11 respectively. The tracks were corrected using a continuous random walk model (R package "crawl"). The deployment site at each colony is indicated by a black square.

4.3 Diving behaviour

Mean dive durations were significantly shorter at DDU than at Davis (Wilcoxon test: W = 165, p-value < 0.05, Table S5.1) and lasted in average 12 ± 0.03 min (max: 84 min) and 13 ± 0.03 min (max: 84 min), respectively (Table S5.1). However, the time spent hunting within each dive, did not differ significantly between the two sites. Seals spent 7 ± 0.03 min (max: 76 min) and 6 ± 0.02 (max: 69 min) min hunting within a dive (Table S5.1) which represented, overall, 61 ± 2 % (max: 72%) and 45 ± 3 % (max: 70 %) of the total time spent diving in DDU and Davis, respectively. Seals from Davis dived significantly deeper (179 ± 0.6 m, max: 1094 m) compared to the seals in DDU (115 ± 0.6 m, max: 904) (Wilcoxon test:W = 193, p-value < 0.05, Table S5.1).

Seals from both sites mostly performed pelagic dives: 66 ± 6 % (max: 91 %) and 71 ± 3 % (max: 89 %) of total dives performed by seals from DDU and Davis, respectively (Table S5.1). The remaining dives were benthic. However, benthic dives represented most of the dives for two individuals: one from DDU (75%, ct47-I-09) and the other one from Davis (69% Awru1-C-06) (Table S5.1). Pelagic dives performed by seals from DDU mostly occurred during the night (43 %), followed by the day (31 %) and twilight (26 %), whereas benthic dives mainly occurred during the day (43 %), followed by the night (30 %) and twilight (27 %) (Fig.5.3). Similarly, pelagic dives performed by seals from the Davis site mostly occurred during the night (52 %), followed by twilight (26 %), instead of by day (22 %), and benthic dives similarly occurred during day (35 %) and night (36 %), followed by twilight (28 %) (Fig. 5.3).

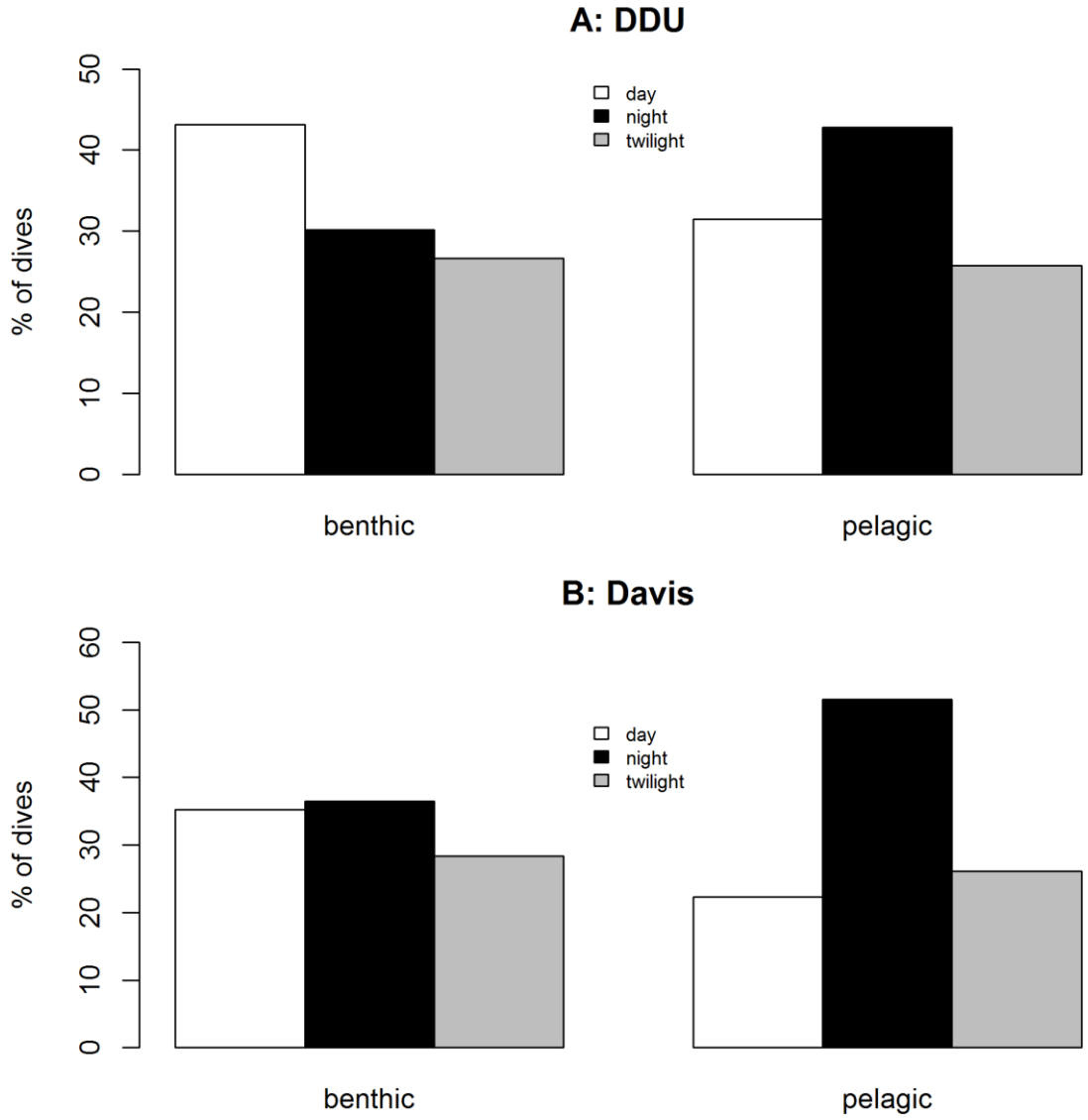

Figure 5.3. Proportion of benthic and pelagic dives performed pooled for all seals from Dumont d'Urville (A) and Davis (B) according to the time of the day (day, twilight and night). Data were pooled from multiple years for each colony.

4.4 Identification of Area-restricted search

4.4.1 Optimal scale differences between FPT and FHT analysis.

All seals exhibited an area-restricted search (ARS) behaviour, although the optimal spatial scales of their search pattern varied between individuals (Fig. 5.4). For seals from DDU, optimal spatial scales obtained from FPT analysis ranged from 0.5 to 6.5 km and were, on average, half that (2.5 ± 0.5 km; Wilcoxon test: $W = 112$, p-value < 0.05) obtained

from FHT analysis (5 ± 1 km) that ranged from 0.5 to 15 km (Table S5.2). For the seals from Davis, optimal spatial scales obtained from FPT analysis ranged from 0.7 to 15 km and were, on average, similar (4.9 ± 0.9 km) to optimal spatial scales obtained from FHT analysis (4.6 ± 1 km) that were ranging from 0.5 to 15 km (Table S5.2).

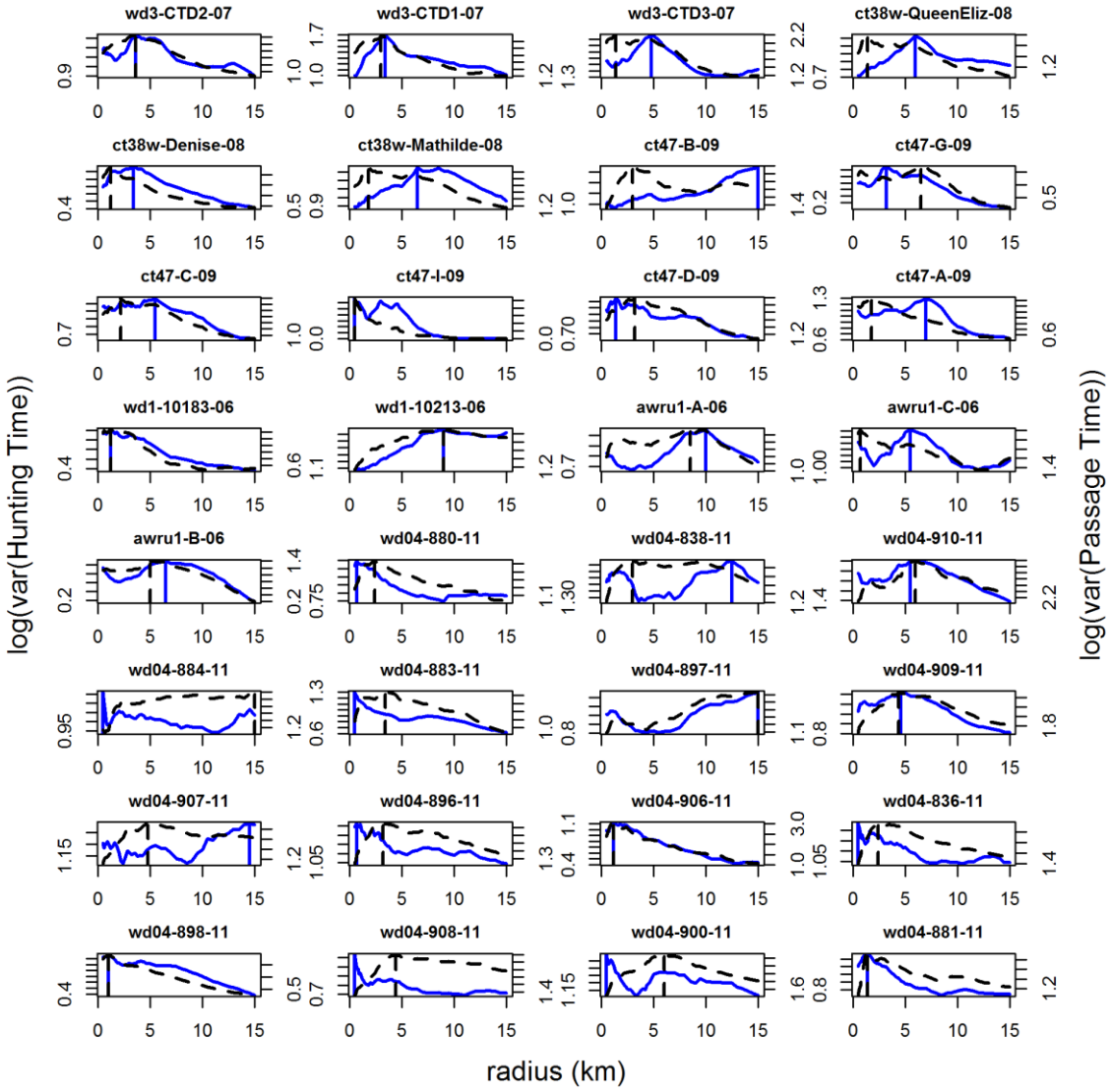

Figure 5.4. Variance in First-Passage Time (FPT) analysis (dotted black line) and in First-Hunting Time (FHT) analysis (blue line) as a function of circle radius for each individual. The maximum peak in variance indicates the scale of the most intensive search behaviour and is indicated by a vertical dotted (FPT) or blue line (FHT).

The FPT analysis is only based on the surface locations of the dives while the FHT analysis also integrates a vertical metric of foraging (*i.e.* hunting time). The difference in optimal spatial scales obtained from both analysis for the seals from DDU, reveals that surface movement patterns of these seals do not reflect their underwater hunting behaviour. Although comparing FPT values from the two sites is interesting this was not the purpose of this study and therefore only FHT values were considered in further analyses.

4.4.2 First hunting time differences between DDU and Davis sites

Average optimal spatial scales of ARS estimated from our FHT analysis were similar in both sites (see above and Table S5.2). However, seals from DDU, spent 2.4 times longer (Wilcoxon test: w= 44, p-value < 0.05) hunting at a given scale (24 ± 0.2 hour, max: 123 hour) compared to seals from Davis (10 ± 0.1 hour, max: 216 hour) (Table S5.2). Similarly, the FHT threshold, used to discriminate "transit" from "hunting" behaviour, of seals from DDU was 2.8 times longer (Wilcoxon test: w= 38, p-value < 0.05; 11 ± 3 hour, max: 45 hour) than for seals from Davis (4 ± 2, max: 32 hour) (Table S5.2). However, similar proportions of dives were associated to each behavioural mode at both sites. Seals from DDU performed 47 ± 3 % (max: 73 %) transit dives and 53 ± 4 % (max: 72 %) hunting dives (Table S5.2, Fig.5.5 a), while seals from Davis performed 45 ± 2 % (max: 60 %) transit dives and 46 ± 3 % (max: 78 %) hunting dives (Table S5.2, Fig.5.5 b).

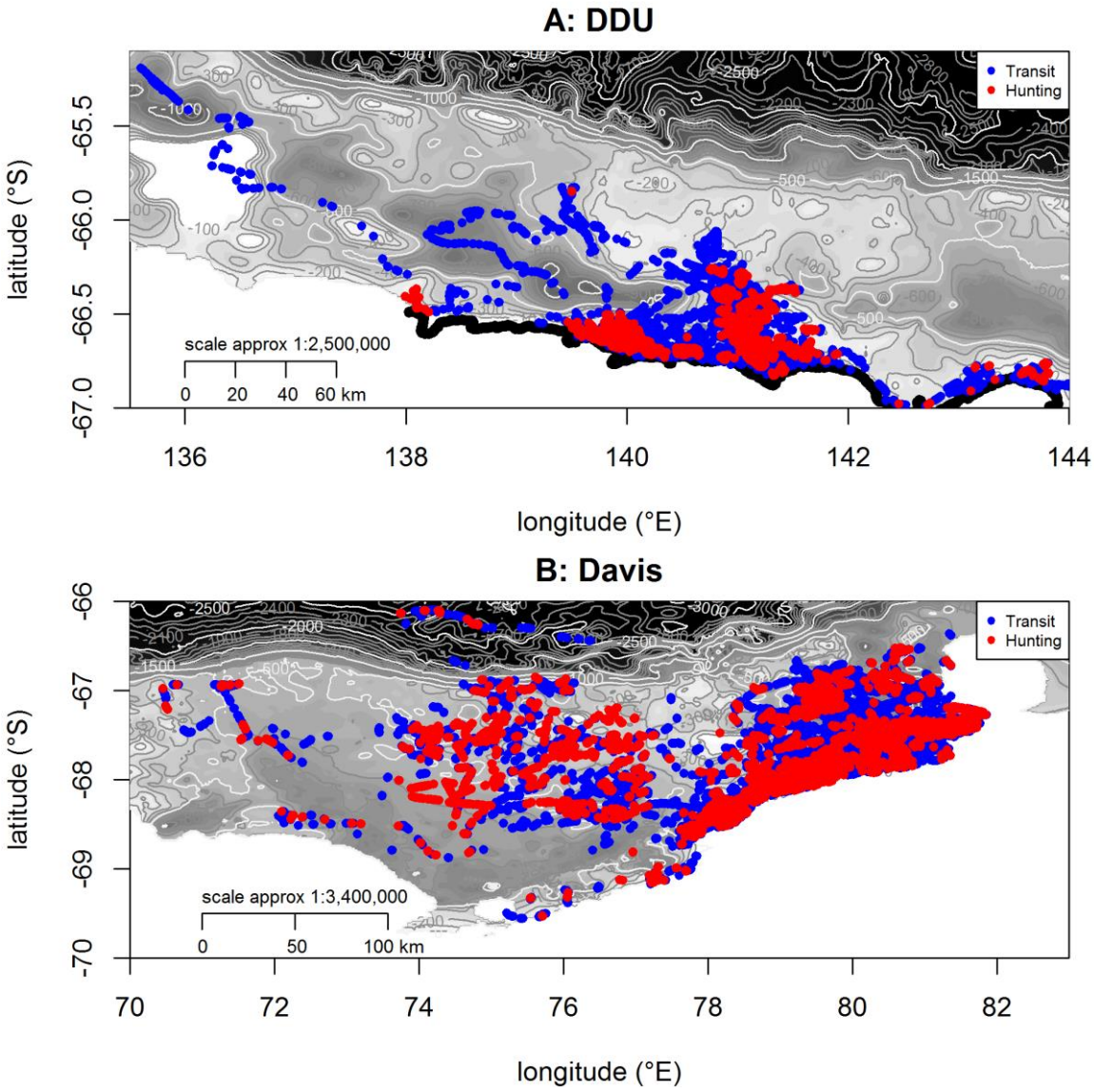

Figure 5.5. Dives of seals from each colony assigned with a behavioural mode according to FHT analysis (i.e. transit and hunting): (A) Dumont D'Urville and (B) Davis colonies over multiple years.

4.5 Area-restricted search behaviour

4.5.1 Diving behaviour associated with "transit" and "hunting" behaviour

Weddell seals in DDU dived to 100 ± 10 m (max: 684 m) and 84 ± 9 m (max: 226 m) and associated dives durations were similar with values of 11 ± 0.4 min (max: 53 min) and 11 ± 0.5 min (max: 84 min) while in transit and hunting mode, respectively (Table S5.3). Huntin time within each dive was 1.3 times longer (Wilcoxon test: W = 108, p-value < 0.05) in hunting dives (8 ± 0.4 min) than in transit dives (6 ± 0.4 min) (Table S5.3). Seventy percent of transit dives were pelagic (Fig.5.6 a). Similarly, 66 % of hunting dives were pelagic (Fig.5.6 a).

Seals from Davis dived to 150 ± 11 m (max: 875 m) and 156 ± 11 m (max: 376 m), while in transit and hunting mode, respectively (Table S5.3). Hunting dives were longer (Wilcoxon test: W = 307, p-value < 0.05; 13 ± 0.5 min) than transit dives (11 ± 0.4 min) (Table S5.3). Furthermore, the time spent hunting within hunting dives was 1.8 times longer (Wilcoxon test: W = 343, p-value < 0.001; 11 ± 0.4 min) than within transit dives (7 ± 0.3 min) (Table S5.3). Seventy-eight percent of transit dives were pelagic and the other 22 % were benthic (Fig. 5.6 b). For hunting dives the disparity was attenuated with pelagic and benthic dives representing 66 % and 34 % of the dives respectively (Fig. 5.6 b).

Seals from Davis dived significantly deeper (Wilcoxon test: transit: W = 192, p-value < 0.05, hunting: W = 213, p-value < 0.001) and spent more time hunting within a dive than the seals from DDU while performing either transit or hunting dives (Table S5.3). Seals from Davis also dived for longer (W = 176, p-value < 0.05) compared to seals from DDU while performing hunting dives, but dive durations were similar while performing transit dives (Table S5.3).

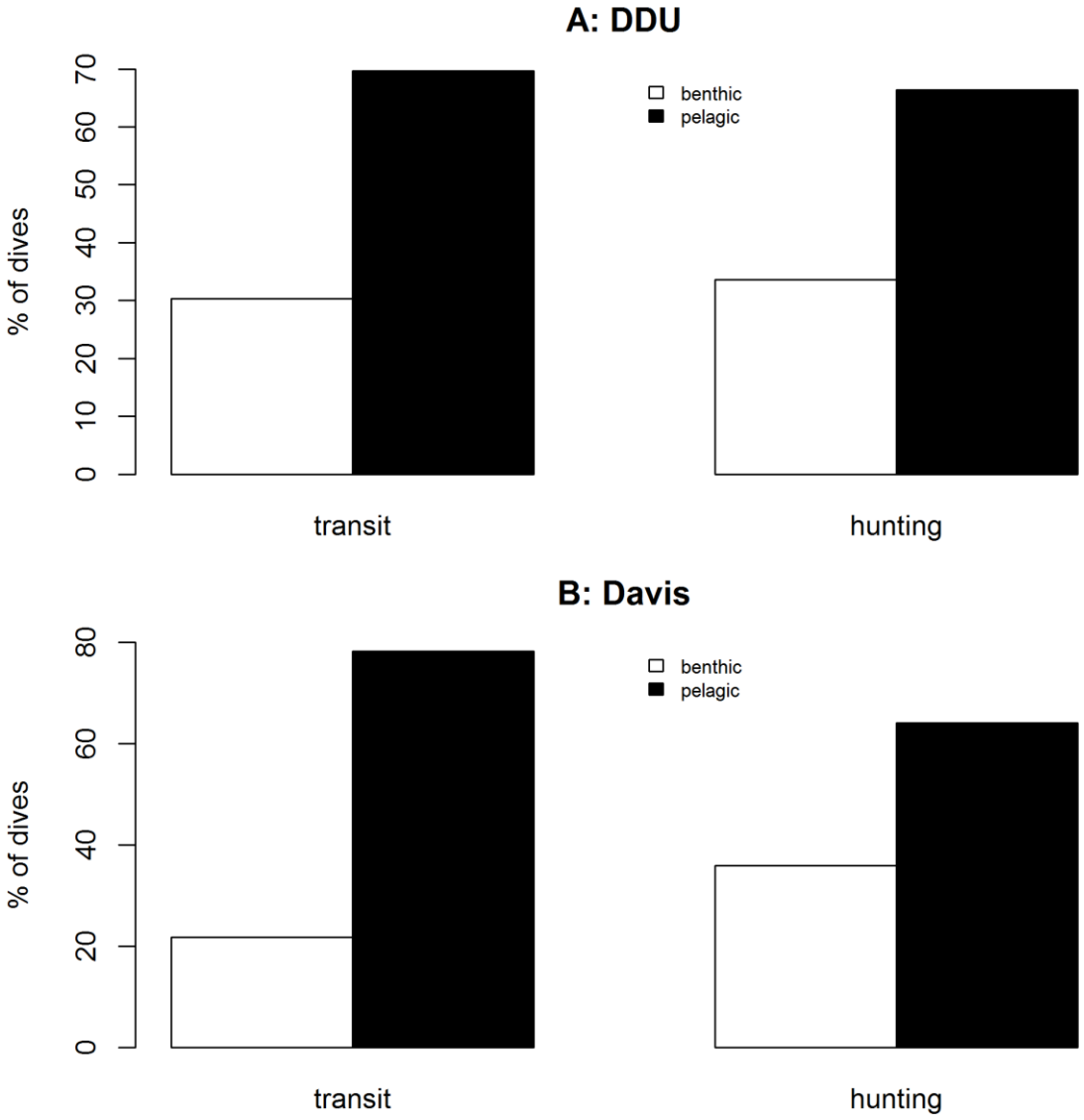

Figure 5.6. Proportion of benthic and pelagic dives performed pooled for all seals from (A) Dumont d'Urville and (B) Davis according to behavioural mode (*i.e.* transit or hunting). Data were pooled from multiple years for each colony.

4.5.2 Spatial distribution of behavioural modes

Overall, hunting dives performed by seals from DDU were aggregated in specific areas whereas transit dive distribution was more dispersed (Fig.5.5 a). In contrast, both hunting and transit dives performed by seals from Davis were more dispersed and occurred in similar areas (Fig.5.5 b). To gain a better understanding of areas used in each behavioural mode, dives were divided into classes according to an individual's maximal distance

travelled from the deployment site. Four and three maximal distance classes were identified in DDU and Davis, respectively (see Fig.S5.3), defining distance-based groups described below.

Seals from DDU travelling less than 140 km from the deployment site mainly used the area on the western side of the Astrolabe glacier between the coast and the D'Urville Trough (140°E), performing both hunting and transit dives (Fig.5.7 a-d). Specifically, transit dives performed by seals travelling between 30 and 140 km from the deployment site were also spread around the edges of the D'Urville trough which enveloped a secondary concentration of hunting dives (141 °E, Fig.5.7 c and d). For the individual travelling between 140 and 220 km, two main areas east of the colony (140 to 144°E) were used during transit, but only the western one (140 to 142 °E) was also used during hunting and divided into four smaller hotspots (Fig.5.7 e and f). For the individual that travelled beyond 220 km from the deployment site, transit dives were concentrated along the coast (138.5 to 141°E), also spreading across the D'Urville trough (Fig.5.7 g). Areas of hunting dive activity (140 and 141°E) were enveloped by transit dive activity and were smaller and also concentrated between the trough edges and the coastline in shallow waters (Fig.5.7 h).

Seals from Davis travelling less than 120 km from the deployment site mainly used two coastal areas (77.75°E and 78.5°E) while performing both transit and hunting dives (Fig.5.8 a and b). Seals travelling between 120 and 300 km from the deployment site used three areas, with both transit and hunting dives coinciding within the two minor patches (68°S 79.5°E and 67°S 79.5°E, Fig.5.8 c and d). However, the main hunting hotspot (n = 12) was located in a cove in the vicinity of a recurring coastal polynya (68.7°S 81.6°E, Fig.5.8 d and Fig.S5.4) northwest of the main transit patch (68.5° 80.2°E, Fig.5.8 c). For the two seals travelling more than 300 km from the deployment site, the main transit and hunting areas were dissociated (Fig.5.8 e and f). Transit dives mainly occurred along the

coast (78.3 to 80.2°E, Fig.5.8 e), whereas hunting dives were mainly offshore in shallow shelf waters west of the transit dive activity (67.6°S 76.9°E, Fig.5.8 f).

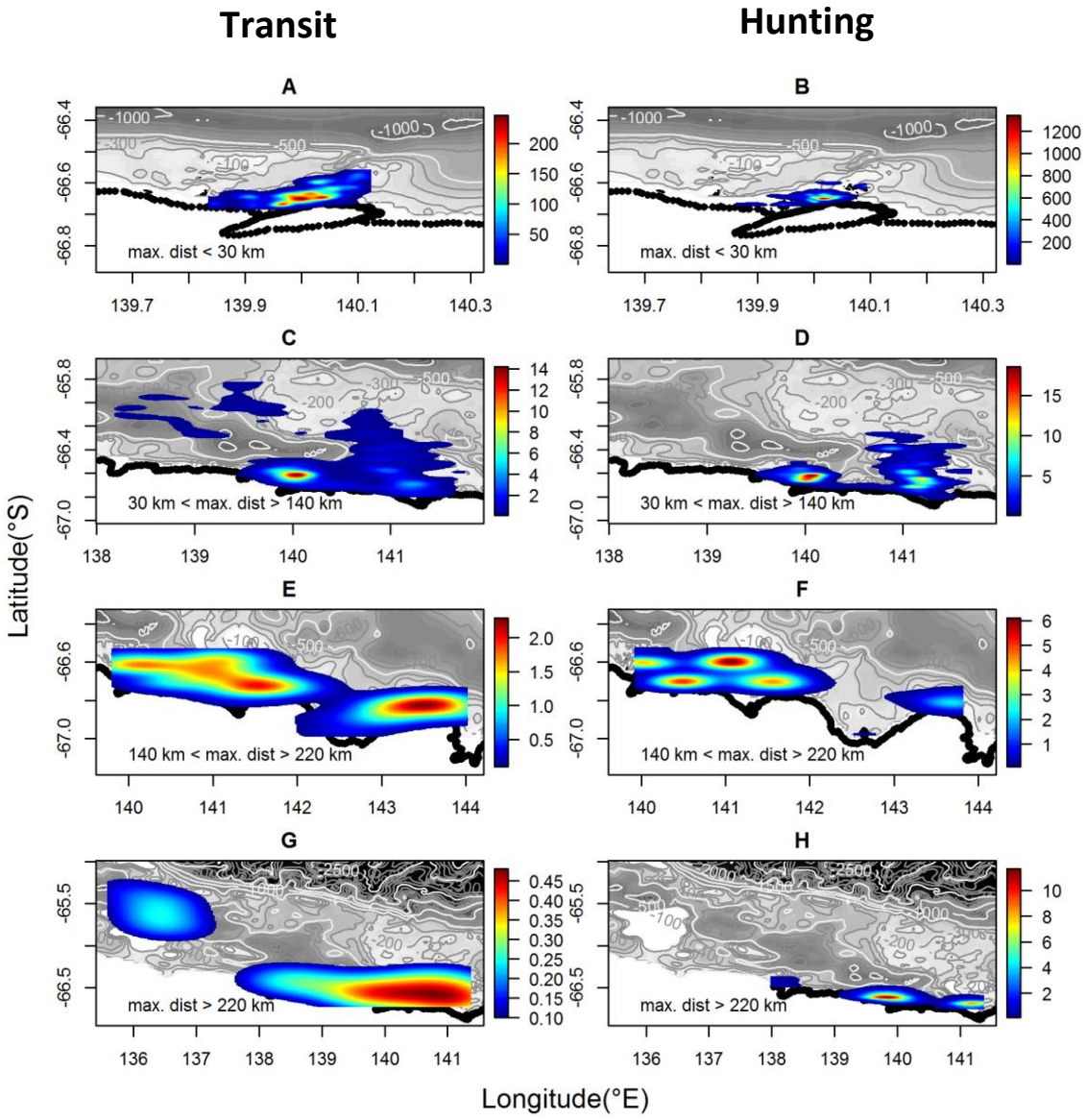

Figure 5.7. Kernel density maps of dive locations from the Dumont D'Urville colony seals (n=12) according to behavioural mode (i.e. transit and hunting) and the distance class. Distance classes were determined according the density distribution of maximal distance travelled from the colony by each individual (see Fig. S5.3 a). Note that scales are different between distance classes.

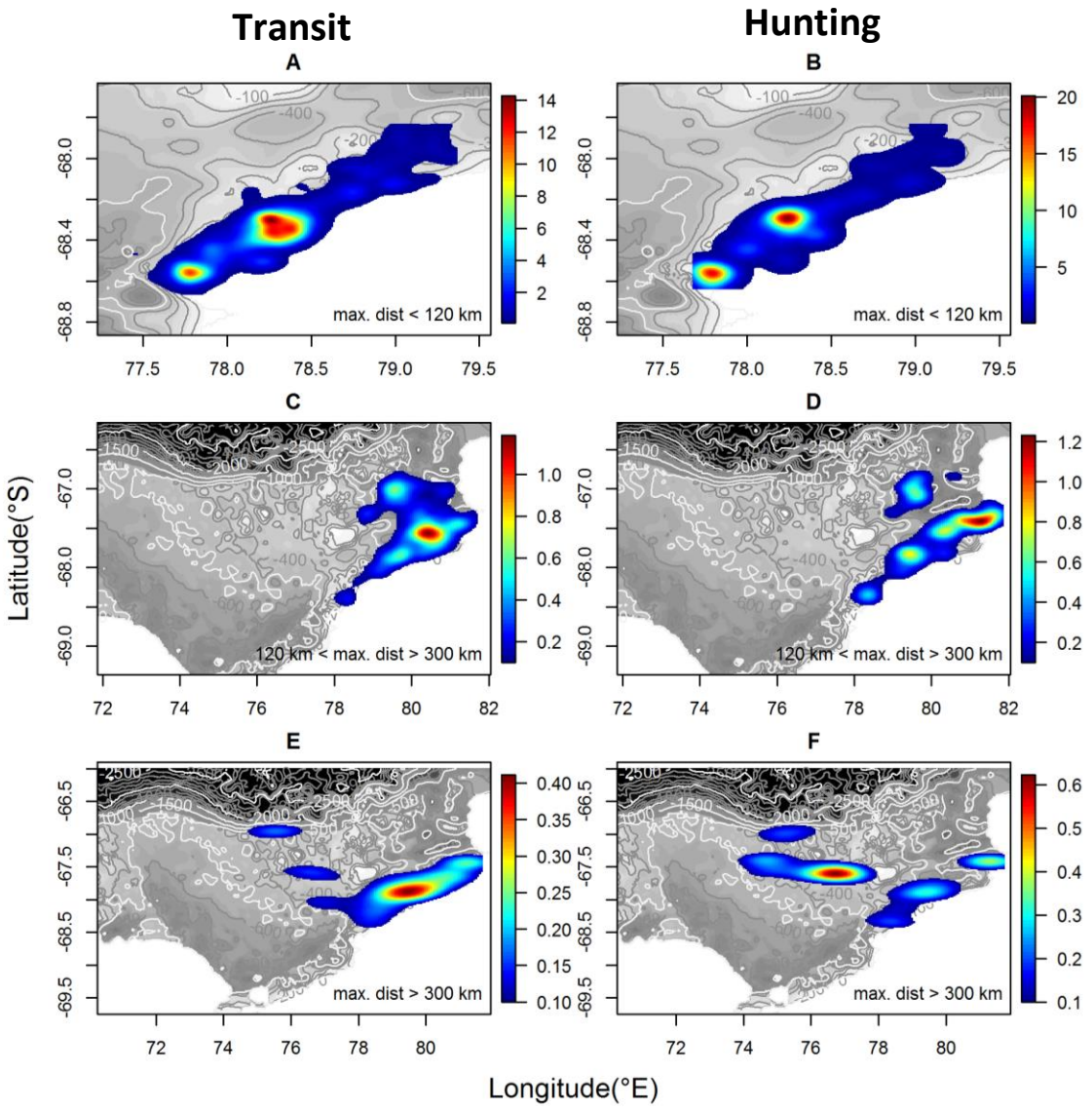

Figure 5.8. Kernel density maps of dive locations from the Davis colony seals (n=20) according to behavioural mode (i.e. transit and hunting) and the distance class. Distance classes were determined according the density distribution of maximal distance travelled from the colony by each individual (see Fig. S5.3 b). Note that scales are different between distance classes.

4.5.3. Habitat use and behavioural mode

Seals from DDU used shallower (Wilcoxon test: W = 118, p-value < 0.05) waters in hunting (158 ± 16 m) compared to when they were in transit (241 ± 27 m) (Table S5.4, Fig.5.9 a and b). However, bathymetric slope and sea-ice concentration at the dives location as well as distance to open-water did not differ significantly (see Table S5.4) between

hunting and transit dives. Seafloor slope associated with hunting and transit dives was 5 ± 0.4 degrees (max: 17 degrees) and 6 ± 0.6 degrees (max: 18 degree) respectively (Table S5.4, Fig.5.9 a and c). Seals used sea-ice concentrations of 60 ± 3 % and 70 ± 5 % that varied over 25 km of 10 ± 2 % and 10 ± 1 % in hunting and transit mode, respectively (Table S5.4). Distances to open water areas were 42 ± 3 km (max: 191 km) and 54 ± 6 km (318 km) in hunting and transit mode, respectively (Table S5.4).

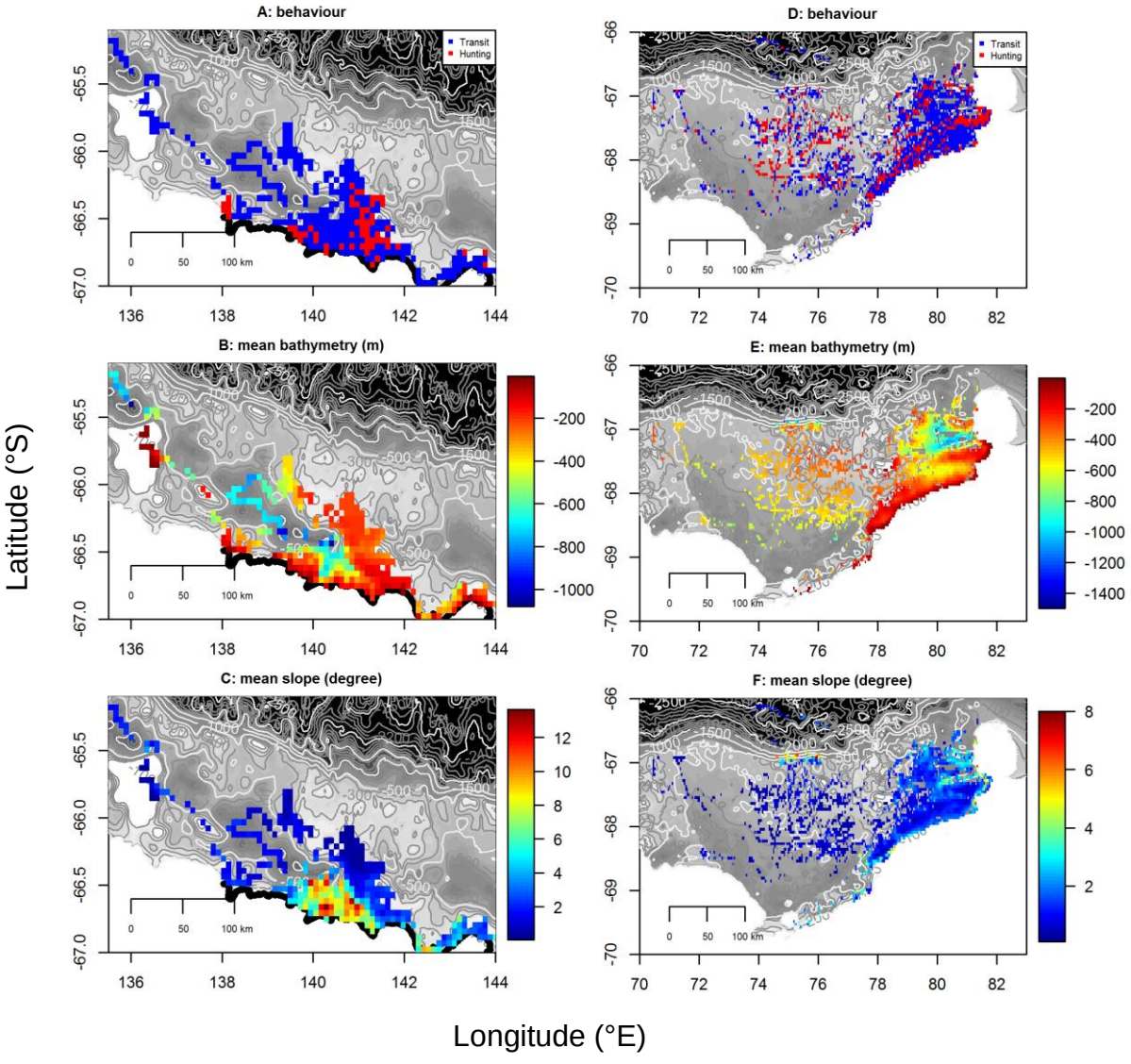

Figure 5.9. Maps of gridded dive locations (5 km x 5 km) for seals from Dumont D'Urville and Davis colonies. Values within each cell are expressed as the most frequent behavioural mode (top); and average value of topographic features according to bathymetry (middle) or bathymetric slope (bottom) within the 25 km² of each gridded location.

Average habitat conditions including bathymetry, bathymetric slope and sea ice variables did not differ significantly (see Table S5.4) between hunting and transit dives performed by the seals from Davis (Table S5.4). The bathymetry used was 309 ± 27 m (max: 2804 m) and 360 ± 31 m (max: 2950 m) associated with seafloor slope of 1 ± 0.1 degree (max: 16 degree) and 1 ± 0.1 degree (max: 12 degree), in hunting and transit mode, respectively (Table S5.4, Fig.5.9 d-f). Sea-ice concentrations were 80 ± 2 % and 70 ± 30 % and associated with variations (over 25 km) of 20 ± 10 % and 20 ± 10 % when in hunting and transit mode, respectively (Table S5.4). Distances to open water areas were 46 ± 5 km (max: 396 km) and 47 ± 5 km (max: 405 km) in hunting and transit mode, respectively.

Seals from Davis significantly used a deeper (Wilcoxon test: transit: $W = 173$, p-value < 0.05; hunting: $W = 207$, p-value < 0.001), smoother (Wilcoxon test: transit: $W = 238$, p-value < 0.001; hunting: $W = 239$, p-value < 0.001) seafloor and were associated with more spatially variable sea-ice (Wilcoxon test: transit: $W = 174$, p-value < 0.05; hunting: $W = 175$, p-value < 0.05) than seals from DDU (Table S5.4). While in hunting mode, sea-ice concentrations encountered by the seals were higher (Wilcoxon test: $W = 219$, p-value < 0.001) in Davis than in DDU (Table S5.4). These results are illustrated in Fig.5.10 where the temporal and spatial use of bathymetry (Fig.5.10 b and f), associated sea-ice concentrations (Fig.5.10 c and g) and variability over 25 km around each dive (Fig.5.10 d and h) are represented. In DDU the sea-ice concentrations and spatial variations did not vary much during winter (Fig.5.10 c and d) and are indicative of a fast-iced coastal area, whereas in Davis highly variable sea ice patterns over winter (Fig.5.10 g and h) reveal typical coastal polynya characteristics (M. Vancopenolle, pers. Com.).

4.5.4 Influence of the environment on behavioural switch

The final model including dive data from both sites showed that the probability of being in hunting mode increased significantly with the advance of winter but decreased with bathymetric depth (in order of importance, see method section 3.6, Table S5.5).

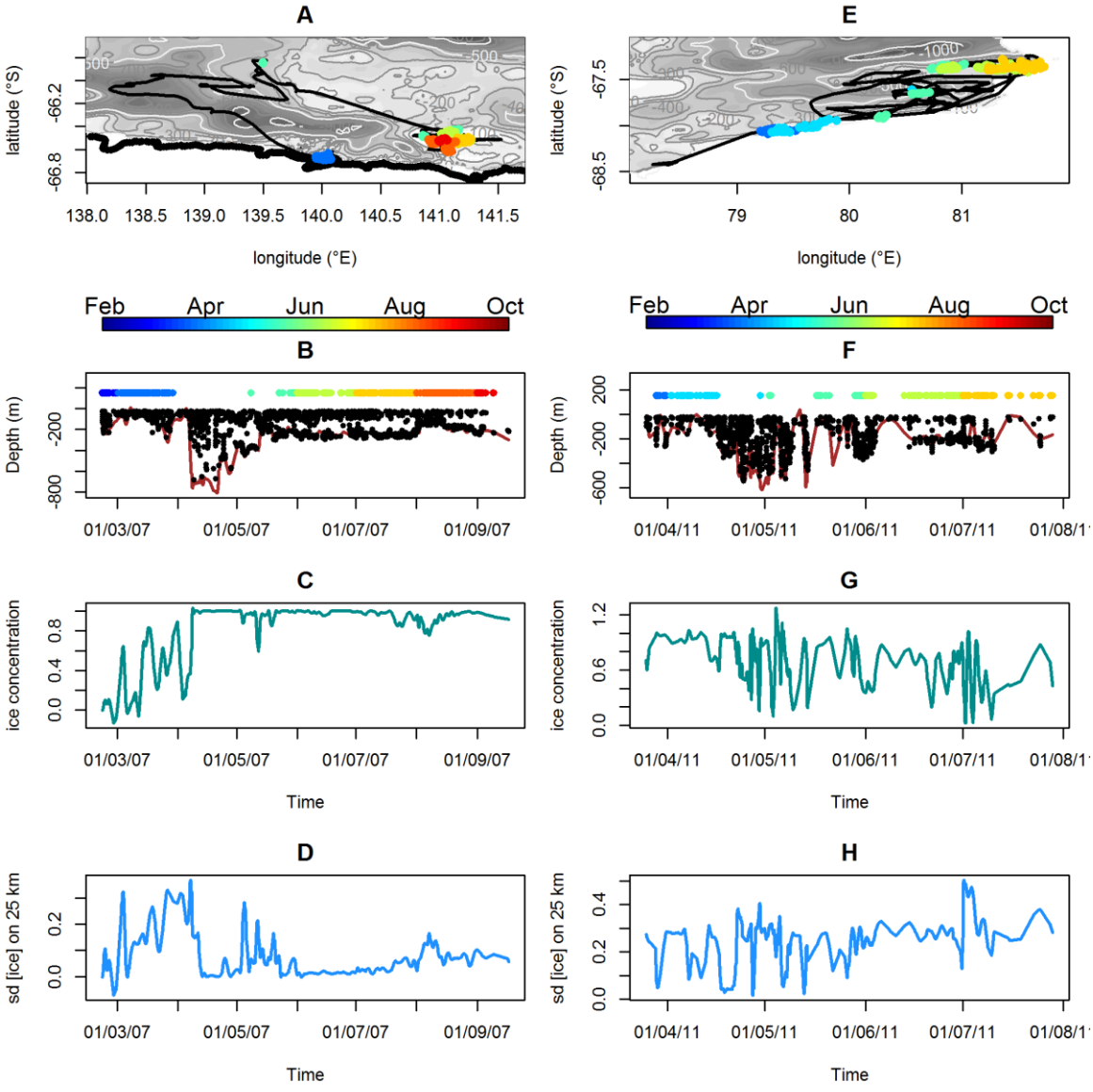

Figure 5.10. Temporal variations of movement patterns and habitat use of an individual seal from each colony: (a-d) Dumont d'Urville and (e-h) Davis. Hunting dive locations are colour coded according to the time of the year (a-b, e-f). Bathymetry, sea-ice concentration and its variation within a radius 25 km for each dive (sd [ice] on 25 km) were extracted and calculated for each dive (see methods section 3.3).

These relationships varied significantly according to the site (*i.e.* DDU and Davis, p-value < 0.001). For instance, the probability of being in hunting mode was positively related to the advance of winter in Davis (coef = 0.58, p-value < 0.001), but negatively related to the advance of winter in DDU (coef = -0.001, p-value < 0.001) (Fig.5.11 a, Table S5.5). At both sites the probability of being in hunting mode decreased when seals used deeper areas,

however, this relationship was stronger at DDU (coef = - 0.0027, p-value < 0.001) compared to Davis (coef = - 0.0013, p-value < 0.001) (Fig.5.11 a, Table S5.5).

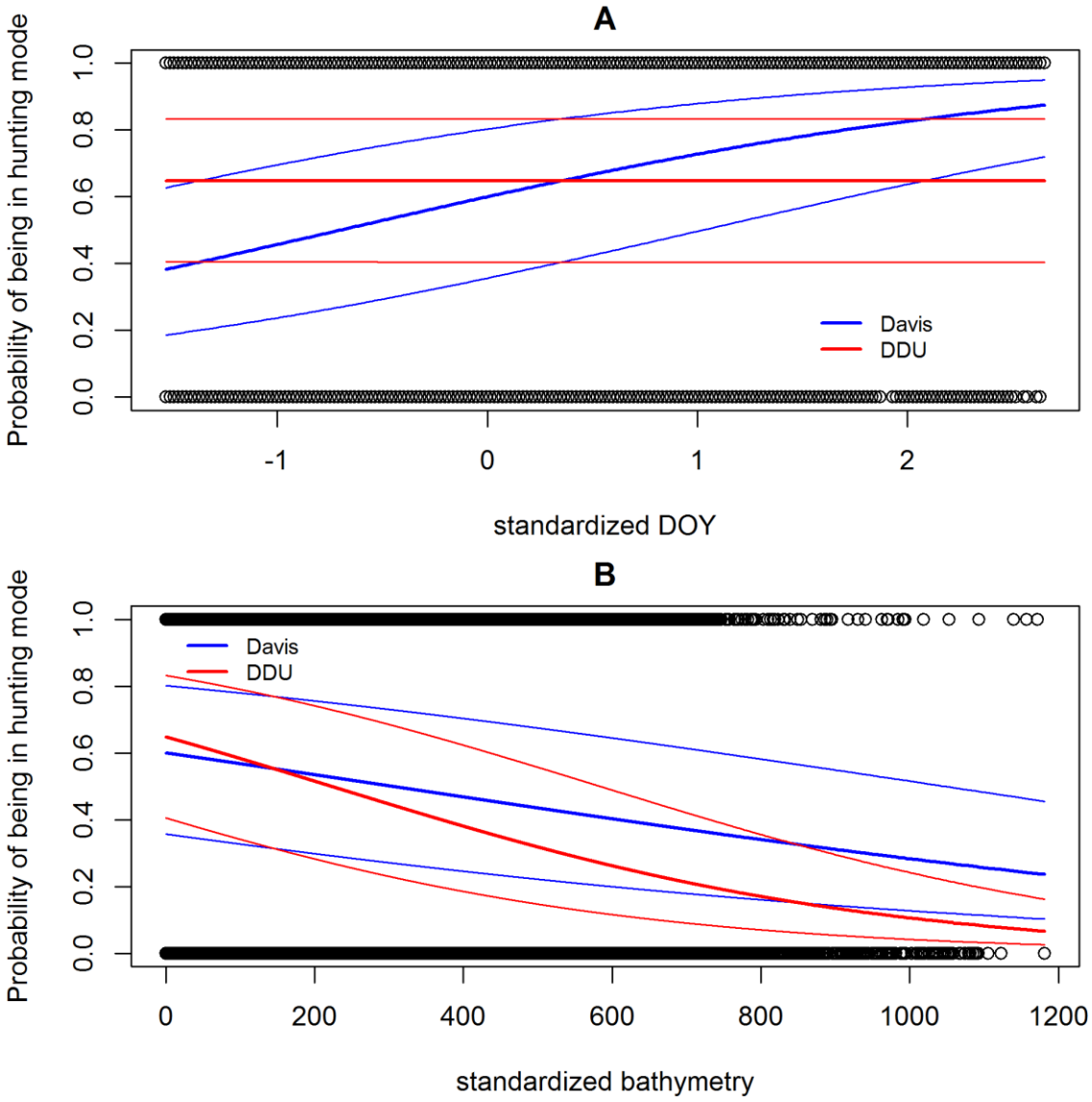

Figure 5.11. The relationship between hunting mode likelihood and (A) day of year (DOY) and (B) bathymetry from our generalized mixed effect models (GLMM). Each model shows the relationship at both colonies: Davis and DDU (Dumont D'Urville). Explanatory variables were standardized to allow comparison of their slope coefficients. For each colony, the thick line in the middle represents the predictive values from the focal population and the two thinner lines represent the boundaries of the variation between the predicted values per individual.

Because there was a "site effect" in the previous model, models were then fitted to each location separately in order to better understand seals' behavioural response to their local environment and its inter-annual variations. In DDU, the probability of being in hunting mode responded significantly to the advance of winter, distance to sea-ice edge and bathymetry (in order of importance, see method section 3.6, Table S5.6). The probability of being in hunting mode increased as winter advanced in 2007-08 (2007: coef = 0.959, p-value < 0.001; 2008: coef = 0.159, p-value < 0.001) but decreased in 2009 (coef = -1.012, p-value < 0.001) (Fig.5.12 a, Table S5.6). The probability of being in hunting mode decreased marginally with the distance to sea-ice edge (coef = -0.06, p-value <0.05) independently of the year (Fig.5.12 b, Table S5.6). Similarly, the probability of being in hunting mode also decreased when seals encountered deeper bathymetry, though this relationship did vary with year (Fig.5.12 c, Table S5.6). The inverse relationship between hunting mode likelihood and bathymetry was similar in 2007 (coef = -0.001, p-value < 0.05) and 2008 (coef = -0.001, p-value = 0.56), but significantly stronger in 2009 (coef = -0.003, p-value < 0.001) (Fig.5.12 c, Table S5.6). Overall, the inter-individual variations were very low (Random effects sd = 0.0016, Table S5.6) resulting in similar intercepts and curve for all individuals (Fig.5.12).

At Davis, the probability of being in hunting mode also responded significantly to the advance of winter and bathymetry, as well as sea-ice spatial variability (Table S5.7). The probability of being in hunting mode increased with the advance of winter (coef = 0.584, p-value < 0.001) but was inversely related to sea-ice spatial variability (coef = -0.06, p-value <0.05) (Fig.5.13 a-b, Table S5.7). These trends were not influenced by year. However, the probability of being in hunting mode, which decreased when seals encountered deeper bathymetry, varied between years (Fig.5.13 c, Table S5.7). The inverse relationship between hunting mode likelihood and bathymetry was similar in 2006 (coef =

-0.001, p-value < 0.05) and 2007 (coef = -0.001, p-value = 0.56), but significantly stronger in 2011 (coef = -0.003, p-value < 0.001) (Fig.5.13 c, Table S5.7). Overall, the inter-individual variations were noticeable (random effects sd = 0.445, Table S5.7) resulting in a range of intercepts according to the individual (Fig. 5.13).

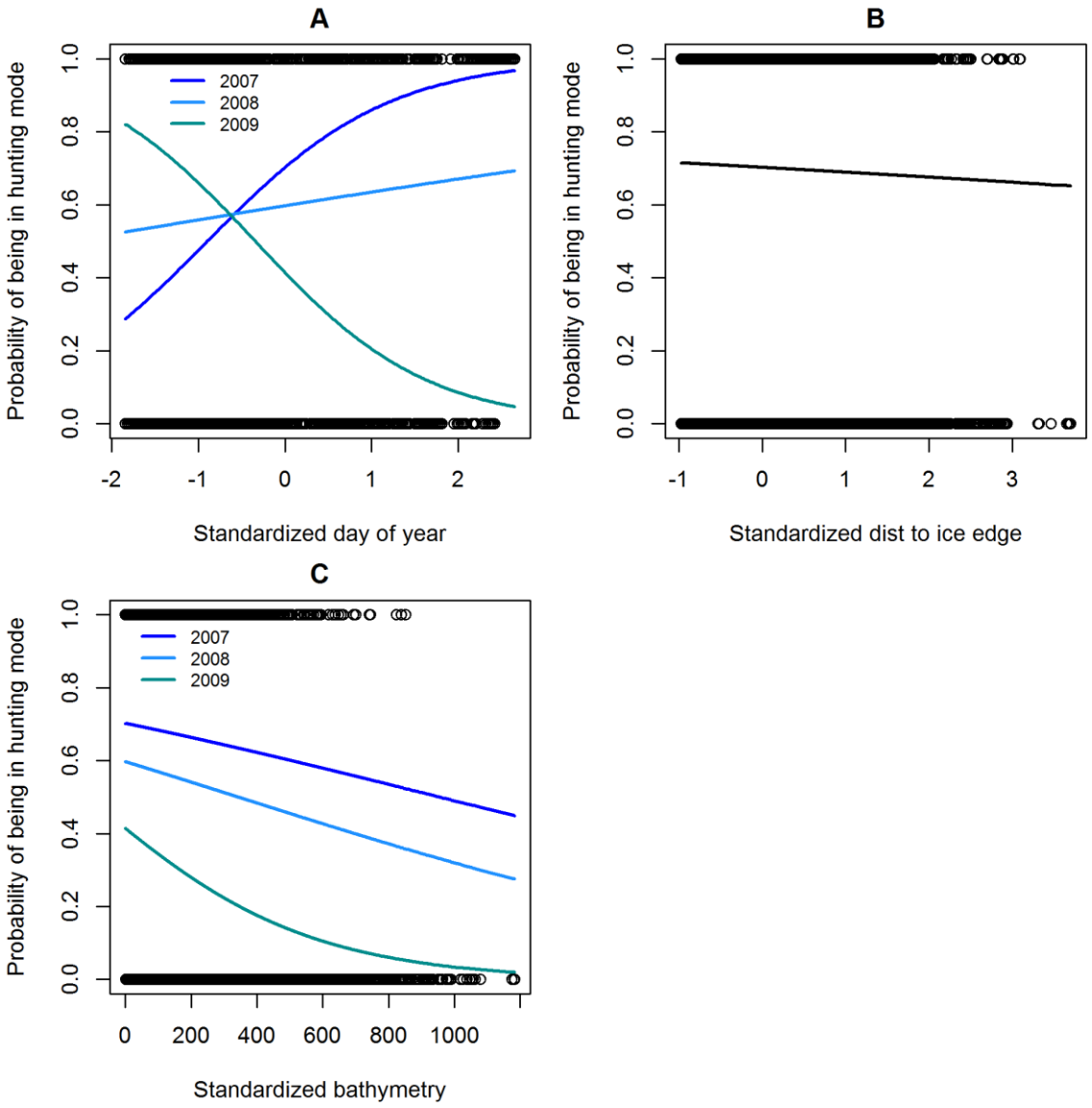

Figure 5.12. The relationship between hunting mode likelihood and (A) day of year [DOY], (B) distance to open water [*i.e.* sea ice concentrations below 20%], and (C) bathymetry from our generalized mixed effect models (GLMM). Data were collected from the Dumont D'Urville site. The relationship between hunting mode likelihood and bathymetry; and hunting mode likelihood and DOY varied according to year. Explanatory variable were standardized to allow comparison of their slope coefficients. The thick line in the middle representing the predictive values for the focal population and the two thinner lines representing the boundaries of the variation between the predicted values per individual are overlapping.

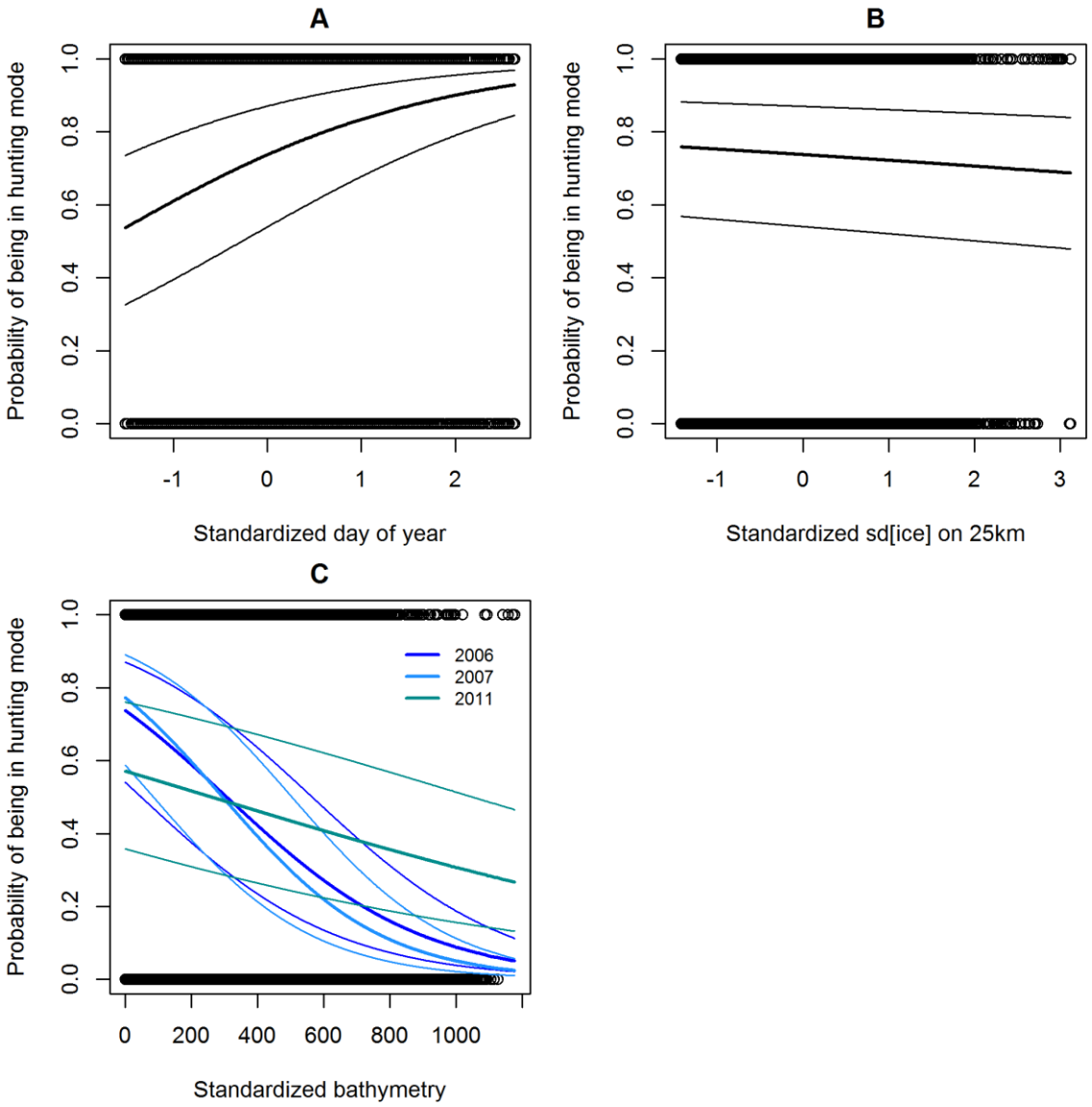

Figure 13. The relationship between hunting mode likelihood and (A) day of year [DOY], (B) the variation of sea-ice concentration within 25 km around each dive, and (C) bathymetry from our generalized mixed effect models (GLMM). Data were collected from the Davis site. The relationship between hunting mode likelihood and bathymetry varied according to year. Explanatory variable were standardized to allow comparison of their slope coefficients. The thick line in the middle represents the predictive values for the focal population and the two thinner lines represents the boundaries of the variation between the predicted values per individual.

5. Discussion

This is the first study comparing the winter foraging behaviour and habitat use of two populations of Weddell seals in East Antarctica. Taking a comparative approach to foraging ecology highlights important factors influencing foraging decisions that would not be apparent from studying a single site. In addition, by integrating a vertical index of the time spent foraging within each dive (*i.e.* hunting time) into a track-based method we identified intensive foraging activity (*i.e.* "hunting" mode) taking into account the 3D movements of the focal Weddell seals. This allowed to investigate the influence of environmental features on focal Weddell seals' foraging decisions. Weddell seals from DDU and Davis showed a high inter-individual variability in their diving behaviour and movement patterns within and between sites. Despite these differences, seals from both sites predominantly used the shallow waters of the Antarctic shelf, staying close to the coast in areas associated with highly concentrated ice. On average, 50% of the dives occurred in ARS and in both locations the switch toward hunting behaviour was influenced by some key environmental features, such as the bathymetry, sea-ice derived metrics (*i.e.* distance to ice edge, spatial variability of sea-ice) and the advance of winter.

5.1 Methodological discussion

5.1.1 Identification of ARS with the FHT analysis

State-space models (SSMs) are a powerful tool used to detect Area-restricted search (ARS) patterns in a range of species (Jonsen *et al.* 2005, 2007, 2013; Dragon *et al.* 2012b; Schick *et al.* 2013). However, when applied to Weddell seal tracks, more than 80 % of the dives were associated with "hunting" behaviour, which is likely related to the species small

scale, highly sinuous displacement, rather than reflecting their true foraging activity (Andrews-Goff *et al.* 2010, V. Andrews-Goff, S. Bestley, *unpublished* data). First-passage time (FPT) provides the optimal scale of increased search effort (Fauchald & Tveraa 2003). However, it calculates the overall time spent in a given area and cannot discriminate between foraging and other activities, such as haul-out periods between dives. Bailleul *et al.* (2008) incorporated diving behaviour (*i.e.* the residuals of the dive bottom time) into the FPT analysis in order to improve this metric. However, recent studies demonstrated that using the bottom time as an index of foraging effort could be inaccurate and misleading (Heerah *et al.* 2014, Paper 3). Heerah *et al.* (2014) developed a "hunting method" that depicts parts of a dive where seals intensified their foraging behaviour (*i.e.* "hunting" parts) where most prey interaction occurred. The hunting time (*i.e.* total time spent in "hunting" parts) allow time spent foraging within a dive to be quantified. Thus, it represented a good metric to integrate in FPT analysis to identify profitable areas within the water column (*i.e.* FHT, see methods section 3.5.2).

According to FPT analysis, the mean ARS optimal scale observed at DDU was smaller than at Davis (DDU: 2.5 km, Davis: 4 km). Results showed that the optimal scales calculated from both FPT and FHT analyses were similar in Davis but different in DDU. On the contrary, similar optimal scales were obtained for both sites when using the FHT analysis (~ 4 km). We also observed sea-ice was more stable and seals were more resident in DDU than in Davis. On the Antarctic shelf, surface movements can be constrained by sea-ice resulting in smaller scale surface movements than what they actually are underwater (*i.e.* where prey encounters occur). Different ice conditions in different locations could change the manner Weddell seals horizontally use their environment, meaning a bias towards search activity in heavy sea ice if using FPT analysis only. Consequently, their horizontal distribution may not truly reflect their vertical foraging behaviour. For marine

predators evolving in a sea-ice environment, it is therefore important to take into account the vertical dimension when defining ARS as previously suggested by Bailleul *et al.* (2008).

5.3.2 Integration of FHT in habitat use models

Although we have demonstrated its purposeful application, the use of the FHT metric in habitat models has its challenges. First, using FHT as a continuous response variable in statistical habitat models is difficult because it violates the assumptions underlying traditional parametric models such as Gaussian generalized linear models (GLMs) (Freitas *et al.* 2008). Similarly, FPTs have been previously used to model habitat use by alternatively using mixed-effects Cox proportional hazards models (CPH model) (Freitas *et al.* 2008). However, the development of CPH models is very recent and does not include temporal covariance terms (Freitas *et al.* 2008). To deal with serially correlated data one should ensure that the temporal resolution of the data is sufficiently coarse to result in independent residuals. Due to the small scale of Weddell seal foraging behaviour the aim was to define their habitat use at the finest scale possible. Instead, we transformed the FHTs into a binary variable (see Freitas et al. 2008) using a FHT time threshold and included it in a binomial mixed effect model for which the addition of an auto-correlation term is possible (see methods section 3.5.2 and 3.6). The defined threshold used to discriminate "search" and "transit" behaviours could be considered a disadvantage. However, this approach is commonly adopted in studies using either FPT or SSM techniques (Jonsen *et al.* 2007; Pinaud & Weimerskirch 2007; Thums *et al.* 2011; Bestley *et al.* 2012).

5.2 Foraging strategies of the focal Weddell seals

5.2.1 Diving Behaviour

Weddell seals from both sites used the entire water column, performing both benthic and pelagic dives (*see also* Plötz *et al.* 2001; Hindell *et al.* 2002; Heerah *et al.* 2012). We also observed a high inter-individual variability in Weddell seals diving behaviour within and between the two sites. These results likely reflect their opportunistic foraging behaviour and diet variations according to the different areas explored. Weddell seals are known to feed on both pelagic prey (e.g. *Pleurogramma antarcticum* and squids), and benthic prey (e.g. shallow *Trematomus* fish species, Antarctic toothfish (*Dissostichus mawsoni*) or crustaceans) (Green & Burton 1987; Castellini *et al.* 1992a; Burns *et al.* 1998; Ainley & Siniff 2009a).

Weddell seals from both sites performed mostly pelagic dives when exhibiting either transit or hunting behaviour. Stable isotope analysis of blood collected from Weddell seals at DDU in winter revealed a pelagic diet of high trophic level (pers. com. Yves Cherel). Pelagic dives were performed mostly at night whereas benthic dives mostly occurred during the day. This suggests, as discussed in Heerah *et al.* (2012), that Weddell seals from DDU are likely to follow the diel migration of their prey according to light intensity. *Pleurogramma antarcticum* is a pelagic fish that aggregates in shoals distributed in different parts of the water column and migrates vertically in direct relation to light intensity (Fuiman *et al.* 2002). At Davis, pelagic dives were also mainly performed at night. However, benthic dives occurred equally during the day and at night. Previous studies reported fine-scale spatial variations in Weddell seals' diet from Davis showing there were several ecotypes of prey within the Vestfold Hills (Green & Burton 1987; Lake *et al.* 2003). Weddell seals foraging in the southern fjords and inshore areas mostly consumed benthic

fishes and prawns, whereas in the northern area and offshore their diet was dominated by *Pleurogramma antarcticum* (Green & Burton 1987; Lake *et al.* 2003). We also showed that Weddell seals from Davis travelled more extensively than seals from DDU. It is therefore likely that, during winter, Weddell seals from Davis fed mainly on pelagic fish such as *Pleurogramma antarcticum* (Green & Burton 1987) but also switched their diet according to where they intensified their hunting effort. Weddell seals in different Antarctic sites can adopt different foraging strategies (restricted hunting dives in DDU vs dispersed hunting dives in Davis) that are likely to be reflected in their diet. The differences between sites also likely reflect different physical characteristics; especially with regards to bathymetric topography (see Green & Burton 1987). Indeed, Weddell seals from Davis dived in deeper waters which resulted in deeper (see Heerah *et al.* 2012) and longer dives, while still displaying similar times spent hunting to the seals from DDU.

5.2.2 Similitudes and differences in foraging strategies of Weddell seals from the two colonies

Despite inter-individual variations, the optimal scale (depicted from FHT analysis), at which Weddell seals conducted their hunting behaviour underwater, was on average similar at both sites (~ 4-5 km radius). This scale corresponds to the distances a seal can travel under-water from a single breathing-hole (Kooyman 1981; Davis *et al.* 2012). It is likely that seals increased the time spent hunting from one hole to maximize prey acquisition before hauling out or moving to another area. In terms of movement patterns, Weddell seals from DDU were much more sedentary than the seals from Davis. The DDU seals tended to travel less distance per day, remain in the vicinity of the deployment site and also stayed closer to the coast. Moreover, seals from DDU spent 2.4 times more time

hunting at a given scale and the time threshold used to discriminate the foraging behaviour was 2.8 times longer. As a result, hunting dives in DDU were constrained in small and shallower areas at the edges of the D'Urville trough. Weddell seals from Davis, in contrast, were more transient and their hunting dives were more dispersed over the shallow areas of the shelf.

Top predators typically do not select areas to feed at random but rather favour ones that are more likely to be associated with increased food availability (Fauchald & Tveraa 2003). This implies that the animals either have some experience of the area, or that they can associate environmental cues with prey density. Thus, our results suggest that the Weddell seals from DDU and Davis adopted different strategies to find breathing holes associated with prey availability. The seals at Davis probably travelled from one hole to another exploring different areas, which has already been observed at this site (Lake *et al.* 2005). In contrast, the movement of seals at DDU was restricted to small specific areas where they probably dived from holes not far from each other or along tide cracks in the ice. Moreover, time series of sea-ice concentrations used by the seals and its spatial variation showed that sea-ice varied more over-winter in Davis than in DDU. This is concordant with the fact that The Vestfold hills (main site of Davis) has been recognized as a marine area of recurring open water adjacent to the coast, identified as a coastal polynya (Worby *et al.* 1998). It is estimated to be eight times larger than the coastal polynya that persists near DDU (Arrigo & Van Dijken 2003). Consequently, two hypotheses emerge from these observations: (i) Weddell seals in DDU moved less because winter sea-ice was heavier and less variable (compared to Davis), thereby constraining their movements or (ii) they used a restricted area likely associated with abundant and predictable prey availability.

Moving in heavy, stable ice can represent a higher risk of disorientation and DDU seals could have had to completely abrade the less-variable sea-ice with their teeth.

However, at other sites, Weddell seals showed their ability to travel under thick ice to reach the thinner pack ice where they foraged (Testa 1994a). In addition, despite the sea-ice conditions, three DDU seals from this study travelled away from the main foraging grounds to explore other areas including the D'Urville Trough and the polynya east of DDU (142-144 °E). The Weddell seal travelling to within the polynya mostly performed transit dives and relatively few hunting dives, only to then return to main foraging area (*i*.e. in front of DDU). These observations suggest that Weddell seals can travel under-thick ice if they need to but in DDU they probably occupy an area that offers the best compromise for both breathing and foraging. In contrast, Weddell seals at Davis could travel to distant areas more easily due to the sea-ice landscape and probably switched from one area to another according to prey availability.

5.2.3 Importance of the winter advancement on foraging effort

Our results showed that the probability of being in hunting mode increased with the advance of winter, with the exception of 2009 (which corresponds to a year with 50% of individuals being adult males). It means that Weddell seals would spend increasingly more time hunting in a given area throughout winter. Winter is of course a critical time for female Weddell seals since it coincides with their gestation period. Thus, during winter, they must maximize food acquisition to ensure healthy pup weights at birth (Kooyman 1981), and also build energy reserves for pup rearing (while also fasting simultaneously) (Cornet & Jouventin 1980; Castellini *et al.* 1992b; Wheatley *et al.* 2008). Andrews-Goff *et al.* (2010) demonstrated that Weddell seals from DDU and Davis decreased the number of haul-outs across winter as air temperature dropped and wind speed increased. Andrews-Goff *et al.* (2010) also suggested that decreased haul-out events could be indicative of an

intensification of hunting behaviour to face winter prey depletion. For instance, female fur seals (*Arctocephalus gazella*) were observed to increase foraging trip duration and activity at times of low prey abundance (Boyd *et al.* 1994). Meiners *et al.* (2012) showed that primary production associated with sea-ice builds in spring (SON) and peaks in summer (DJF), only to decline in autumn (MAM) and reaches minimum levels in winter (JJA).

It is likely that the combination of these different factors resulted in seals spending more time diving to avoid harsh winter weather conditions and maximize prey acquisition before the breeding season. In this context, Weddell seals likely optimized their foraging strategy by: (i) minimizing the costs associated with travel between prey patches as sea-ice thickens during winter by increasing their hunting effort in a given area; and (ii) favouring environmental conditions likely to be associated with increased prey availability and accessibility (as discussed below).

5.3 Habitat use

5.3.1 Sea ice environment

Lake *et al.* (2006) suggested that the sea-ice landscape in the Vestfold Hills would allow the Weddell seals to use the fast-ice to rest but travel further offshore to forage in the pack-ice, a pattern that has also been observed at McMurdo (Testa 1994a). In contrast, Weddell seals from both DDU and Davis used high concentrated sea-ice while performing either hunting or transit dives without significant differences. Sea-ice concentration did not influence their behavioural switch, although seals from Davis were less likely to be in hunting mode as spatial variability of sea ice increased. Although this result is surprising, it might indicate that to forage, seals prefer stable and more predictable ice features as they will need it to haul-out (Kooyman 1981; Castellini *et al.* 1992b).

The fast-ice environment can be seen as a profitable habitat for a species such as the Weddell seal, capable of inhabiting annual fast-ice both in summer and winter (Castellini *et al.* 1992a; Burns & Kooyman 2001). During the dark Antarctic winter, low productivity persists in open water areas due to light limitation (Arrigo & Van Dijken 2003; Tynan *et al.* 2009). Conversely, sea-ice areas provide reliable food sources as sea-ice algae, the only winter growing phytoplankton is contained within the ice and on the underside of floes (Arrigo 2014). These epongic algae are grazed by zooplankton (such as euphausiids, *i.e.* krill) which in turn are consumed by fish (such as nothoteneids, *i.e.* silverfish) which are the main prey of Weddell seals at DDU and Davis (Green & Burton 1987, Y. Cherel *unpublished data*). Altough focal Weddell seals foraged in fast-ice, seals from both sites remained relatively close to open water areas (*i.e.* ~ 40-50 km) when available. In addition, Weddell seals from DDU were more likely to switch toward a hunting mode if closer to open water. This may not directly influence the availability of prey for Weddell seals but rather denotes the presence of thinner ice areas within the fast ice. Indeed, Weddell seals could favour thinner ice as the maintenance of breathing hole in thick ice can wear their teeth and this has been reported as a significant cause of mortality (Stirling 1969). In addition the seals' pluri-annual residency to similar areas and their proximity to land, suggests that seals were likely to use fast-iced areas where environmental features will sustain the formation of tide cracks (*e.g.* presence of land and islands, input of warmer water, coastal polynias) (Kooyman 1981; Lake *et al.* 2005). The necessity of these tide cracks was emphasised in 2000 at McMurdo Sound when a grounded iceberg prevented the fast ice from breaking up and resulted in a significant decline of the local Weddell seal population (Siniff *et al.* 2008). Foraging under the ice seems to be a subtle trade-off between finding predictable sea-ice-dependent prey and the ability to breathe.

5.3.2 The importance of bathymetry

In our study, Weddell seals from both sites were more likely to switch to hunting behaviour in shallower areas. At DDU, areas associated with transit and hunting dives overlapped, although hunting areas were much more constrained and typically located between the coastline and the edges of the deep D'Urville trough. DDU seals use of the trough was characterized by significantly higher slope values associated with the dives than at Davis. Hunting dives were also significantly associated with shallower waters; a pattern that has already been seen in other seal species (Burns *et al.* 2004; Muelbert *et al.* 2013; Raymond *et al.* 2014). The area surrounding the edges of the D'Urville trough is known area of ecological significance for Adelie (*Pygoscelis adeliae*) and emperor penguins, as well as Weddell seals (Koubbi et al. 2011).

At Davis, two main foraging grounds overlapped with transit movement for seals travelling relatively short distances (*i.e.* less than 120 km). In contrast, the main foraging grounds and transit movement of seals travelling greater distances (*i.e.* from 120 to more than 300 km) were dissociated. Individuals travelling greater distances mainly intensified their foraging effort: (i) in a coastal polynya that persisted throughout winter (see Fig. S5.4), associated with shallow waters and surrounded by bathymetric depressions or (ii) on the shallow areas of the shelf located between two bathymetric depressions.

Weddell seals from both sites seemed to strategically use shallow areas where the bathymetry was likely to interact with other physical features such as the water masses, and ultimately the sea-ice. The trough and depressions surrounding the foraging grounds of the seals could facilitate the upwelling of the warmer, macronutrient-enriched Modified Circumpolar Deep Water (MCDW) onto shallower areas (Tynan 1998; Prézelin *et al.* 2000). This would result in enhanced winter production, but also favour the formation of

fronts where prey would aggregate (Prézelin *et al.* 2000). The presence of the warmer MCDW can also interact with sea-ice dynamics by: (i) facilitating the formation of cracks in the ice and/or (ii) maintaining surface water above freezing, which result in polynias when combined with ideal conditions (*e.g.* strong katabatic winds, presence of glacier, strong tidal forcing) (Arrigo & Van Dijken 2003). At DDU, Lacarra *et al.* (2011) suggested a flow of the MCDW from the D'Urville trough to the coastal zone and the Adelie bank does indeed exist. Heerah *et al.* (2012) also demonstrated that it was the main water mass explored by the Weddell seals in winter at DDU. However, at Davis, direct evidence of seals exploring the MCDW is not available as the tags deployed for this study did not record both salinity and temperature (data necessary for identifying such conditions).

The fact that seal hunting dives were performed over shallower bathymetry instead of the available deeper areas also suggest that these shallower areas could facilitate prey accessibility (see discussion in Burns *et al.* 2004, 2008; Heerah *et al.* 2012). Moreover, Plötz *et al.* (2001) suggested a hunting seal descending from the surface would not switch to benthic foraging as long as *Pleurogramma antarcticum* was available in the upper water column. Seals foraging in shallower areas could switch more easily to benthic prey if their initial prey targets became depleted in the water column.

6. Conclusion

During winter, Weddell seals must fulfil their food requirements to ensure their survival, reproductive and breeding success the following summer. This is the first comparative study on the winter foraging behaviour of Weddell seals in two locations of East Antarctica with distinctly different environmental conditions. We showed that seals adopted different foraging strategies according to these contrasting environments. In the Davis polynya driven system, where access to open water is less restrictive, seals travelled more and hunting distribution was more dispersed. Conversely, in the coastal area of DDU, which is mostly covered by fast-ice, seals were more resident and their fidelity to the same areas suggested the existence of recurring cracks in the ice (Kooyman 1981). However in both locations Weddell seals hunted in highly concentrated ice above shallow bathymetry surrounded by canyons and depressions. It is likely that these habitat selected by the Weddell seals in these contrasting environments are associated with predictable prey availability and accessibility. The complex bathymetry of the Antarctic shelf, via its influence on physical and biological processes, appears to be one of the key aspects to understanding how top predators survive during winter in Antarctic (Chapman *et al.* 2004; Ribic *et al.* 2008). The high variability of diving and foraging behaviours reflects the heterogeneous prey distribution on the Antarctic shelf between and within locations (see Lake et al., 2003). It also highlights the difficulty in predicting Weddell seals' habitat use, which has implications for conservation management. The plasticity of their foraging behaviour and their opportunistic diet reflect their adaptation to the highly seasonal and pluri-annual variable Antarctic environment, and is perhaps one explanation as to why their populations are currently stable (Siniff *et al.* 2008; Southwell *et al.* 2012). However, their obvious need for both stable sea-ice conditions and the presence of apertures in the ice

suggest that changes in sea-ice thickness, extension and seasonal persistence could affect them (see Siniff et al., 2008). This highlights the need for offshore high-resolution sea-ice data and images that encompass the entire winter season to improve our understanding of top predator habitat use on the Antarctic shelf during winter.

7. Acknowledgements

We are grateful to S. Blanc, A. Jacquet-Chaboisson, E. Antoine and all volunteers from the 56th, 57th and 58th scientific missions at Dumont d'Urville who assisted in the field. This study was supported by an Australian Antarctic Science grant (AAS project 2794), and program Terre-Océan-Surface Continentale-Atmosphère from Centre National d'Etudes Spatiales (TOSCA-CNES). We thank the Institut Polaire Français Paul Emile Victor (IPEV programs 109 and 394), Terres Australes et Antarctiques Françaises (TAAF) and the Australian Antarctic Division for providing logistical support. We wish to thank F. bailleul for his advices and help on the use of the FPT and FrBT methods and M. O'Toole for his comments and revisions of the manuscript. Fieldwork and data collection was undertaken with approval from the University of Tasmania Animal Ethics Committee (permit A8523), and from IPEV and TAAF Animal Ethics committee. All animals in this study were cared for according to their guidelines.

8. Appendix

Table S5.1. Trip summary of movements and diving behaviour of Weddell seals equipped with SRDL tags at Dumont d'Urville (DDU) (2007-2009) and Davis (2006-07 and 2011). Most of the individuals were adult females, although the ID of males is coloured in blue. Values are presented as mean ± se (max). Distance to the deployment site is the average of distances between deployment site and each seal position. Distance to the coast is the average of distances between closest positive bathymetric value and each seal position. Distance per day is the average of the distance travelled between the first and last seal locations of each day. Wilcoxon tests were performed to compare mean distances and diving behavioural metrics between DDU and Davis.

Seal ID	Colony	Mass(kg)	Size (cm)	Date of deployements	Duration of deployements (day)	Distance from deployment (km)	Distance per day (km)	Distance from the coast (km)	Number of dives	Number of dives per day	Maximal depth (m)	Dive duration (min	Hunting time (min)	% of benthic dives	% of pelagic dives
wd3-CTD2-07	DDU	307	237	20/02/2007	183	41 ± 0.4 (77)	7 ± 0.5 (42)	25 ± 0.3 (71)	3686	21 ± 1 (82)	163 ± 1 (584)	12 ± 0.1 (38)	7 ± 0.1 (32)	50	50
wd3-CTD1-07	DDU	364	246	20/02/2007	242	32 ± 0.3 (58)	2 ± 0.2 (18)	3 ± 0.04 (9)	3597	16 ± 0.6 (47)	84 ± 1 (584)	13 ± 0.1 (38)	9 ± 0.1 (30)	9	91
wd3-CTD3-07	DDU	339	230	21/02/2007	209	44 ± 0.5 (103)	3 ± 0.3 (30)	23 ± 0.4 (80)	2936	15 ± 0.7 (51)	207 ± 3 (904)	13 ± 0.1 (44)	6 ± 0.1 (29)	46	54
ct38w-QueenEliz-08	DDU	NA	232	21/02/2007	182	27 ± 0.4 (69)	3 ± 0.3 (25)	5 ± 0.1 (22)	2780	16 ± 0.7 (45)	87 ± 1 (524)	11 ± 0.1 (36)	7 ± 0.1 (30)	10	90
ct38w-Denise-08	DDU	NA	223	22/02/2008	234	28 ± 0.5 (56)	1 ± 0.1 (18)	6 ± 0.1 (22)	2639	12 ± 0.5 (45)	111 ± 2 (544)	14 ± 0.1 (39)	9 ± 0.1 (33)	34	66
ct38w-Mathilde-08	DDU	NA	250	23/02/2008	236	39 ± 0.4 (71)	3 ± 0.3 (35)	7 ± 0.1 (21)	2863	14 ± 0.6 (37)	130 ± 2 (804)	13 ± 0.1 (84)	8 ± 0.1 (76)	36	64
ct47-B-09	DDU	262	220	13/02/2009	167	46 ± 1 (258)	12 ± 1 (75)	9 ± 0.4 (98)	1989	14 ± 0.7 (41)	109 ± 2 (604)	10 ± 0.1 (37)	5 ± 0.1 (32)	35	65
ct47-G-09	DDU	218	213	15/02/2009	119	3 ± 0.04 (12)	2 ± 0.2 (8)	1 ± 0.04 (9)	2344	20 ± 1 (65)	64 ± 1 (321)	8 ± 0.1 (23)	5 ± 0.1 (18)	50	50
ct47-C-09	DDU	307	225	17/02/2009	151	19 ± 0.5 (77)	5 ± 0.5 (31)	6 ± 0.2 (48)	1555	11 ± 0.7 (51)	114 ± 3 (664)	12 ± 0.2 (35)	7 ± 0.1 (30)	28	72

ct47-I-09	DDU	299	226	19/02/2009	121	2 ± 0.05 (8)	0.5 ± 0.04 (2)	1 ± 0.03 (5)	1496	13 ± 0.8 (42)	62 ± 1 (206)	10 ± 0.1 (45)	7 ± 0.1 (36)	75	25
ct47-D-09	DDU	217	229	19/02/2009	115	74 ± 1 (178)	11 ± 1 (47)	1 ± 0.03 (5)	2033	18 ± 1 (65)	140 ± 2 (654)	11 ± 0.1 (53)	5 ± 0.1 (46)	23	77
ct47-A-09	DDU	243	228	22/02/2009	197	8 ± 0.07 (42)	2 ± 0.2 (23)	3 ± 0.04 (16)	2401	13 ± 0.6 (38)	73 ± 1 (441)	10 ± 0.1 (42)	7 ± 0.1 (27)	13	87
wd04-880-11	Davis	464	267	11/03/2011	181	132 ± 1 (325)	11 ± 1 (81)	116 ± 1 (293)	3085	19 ± 1 (68)	245 ± 3 (784)	15 ± 0.1 (73)	6 ± 0.1 (69)	41	59
wd04-838-11	Davis	329	240	11/03/2011	122	83 ± 1 (161)	11 ± 1 (54)	17 ± 0.3 (44)	1570	15 ± 1 (57)	135 ± 2 (554)	10 ± 0.1 (71)	5 ± 0.1 (67)	15	85
wd04-910-11	Davis	401	240	12/03/2011	170	86 ± 1 (158)	5 ± 0.6 (35)	20 ± 0.2 (40)	1690	14 ± 1 (51)	192 ± 3 (644)	14 ± 0.2 (62)	7 ± 0.2 (52)	29	71
wd04-884-11	Davis	416	250	12/03/2011	199	96 ± 2 (158)	10 ± 1 (72)	43 ± 1 (184)	1363	14 ± 1 (47)	215 ± 5 (744)	13 ± 0.2 (39)	5 ± 0.1 (28)	37	63
wd04-883-11	Davis	330	239	12/03/2011	137	134 ± 1 (205)	13 ± 1 (59)	17 ± 0.2 (71)	3806	24 ± 1 (74)	226 ± 3 (1094)	15 ± 0.1 (62)	6 ± 0.1 (42)	23	77
wd04-897-11	Davis	367	253	13/03/2011	162	124 ± 1 (236)	17 ± 2 (117)	62 ± 1 (193)	2539	17 ± 1 (62)	185 ± 3 (714)	14 ± 0.1 (49)	6 ± 0.1 (29)	19	81
wd04-909-11	Davis	365	222	25/03/2011	166	133 ± 0.6 (207)	21 ± 2 (144)	48 ± 0.5 (116)	2868	20 ± 1 (70)	258 ± 3 (774)	16 ± 0.1 (68)	5 ± 0.1 (46)	15	85
wd04-907-11	Davis	366	235	25/03/2011	126	134 ± 0.9 (134)	12 ± 1 (73)	10 ± 0.2 (49)	2405	20 ± 0.9 (45)	224 ± 3 (694)	14 ± 0.1 (45)	5 ± 0.1 (35)	36	64
wd04-896-11	Davis	317	250	25/03/2011	142	139 ± 1 (372)	18 ± 1 (83)	30 ± 0.8 (170)	2953	22 ± 1 (71)	183 ± 3 (784)	11 ± 0.1 (56)	4 ± 0.1 (47)	24	76
wd04-906-11	Davis	325	232	25/03/2011	179	43 ± 0.4 (75)	4 ± 0.6 (38)	9 ± 0.2 (31)	1226	10 ± 0.9 (45)	112 ± 2 (346)	9 ± 0.2 (45)	4 ± 0.2 (36)	26	74
wd04-836-11	Davis	322	246	26/03/2011	189	129 ± 0.7 (233)	15 ± 1 (67)	27 ± 0.4 (86)	3277	19 ± 1 (68)	183 ± 2 (714)	12 ± 0.1 (49)	5 ± 0.1 (49)	11	89
wd04-898-11	Davis	298	228	26/03/2011	189	23 ± 0.2 (42)	3 ± 0.3 (19)	6 ± 0.05 (23)	3565	20 ± 0.9 (63)	86 ± 0.6 (306)	11 ± 0.1 (35)	8 ± 0.1 (35)	46	54
wd04-908-11	Davis	339	235	26/03/2011	189	125 ± 1 (214)	11 ± 1 (70)	82 ± 1 (185)	1909	14 ± 1 (51)	204 ± 3 (724)	14 ± 0.2 (84)	6 ± 0.2 (65)	22	78
wd04-900-11	Davis	381	240	27/03/2011	170	151 ± 0.9 (268)	16 ± 2 (76)	36 ± 0.4 (86)	2727	18 ± 1 (81)	244 ± 3 (844)	13 ± 0.1 (40)	4 ± 0.1 (33)	18	82

wd04-881-11	Davis	452	250	27/03/2011	93	169 ± 1 (169)	16 ± 2 (74)	19 ± 0.4 (55)	1282	19 ± 1 (58)	193 ± 4 (694)	13 ± 0.2 (37)	6 ± 0.2 (30)	34	66
wd1-10213-06	Davis	NA	222	7/04/2006	177	165 ± 0.3 (208)	13 ± 0.9 (72)	35 ± 0.5 (91)	4741	27 ± 1 (74)	220 ± 2 (875)	13 ± 0.1 (58)	4 ± 0.1 (47)	11	89
wd1-10183-06	Davis	NA	224	7/04/2006	94	25 ± 0.4 (50)	4 ± 0.7 (46)	6 ± 0.2 (23)	1115	14 ± 1 (58)	121 ± 2 (317)	11 ± 0.2 (34)	6 ± 0.1 (23)	42	58
awru1-A-06	Davis	NA	NA	2/03/2007	118	21 ± 0.2 (40)	10 ± 0.8 (46)	9 ± 0.1 (25)	2459	22 ± 0.8 (51)	111 ± 1 (282)	11 ± 0.1 (31)	5 ± 0.1 (28)	38	62
awru1-C-06	Davis	NA	NA	2/03/2007	179	18 ± 0.1 (33)	5 ± 0.5 (33)	4 ± 0.05 (14)	2834	19 ± 1 (61)	67 ± 0.5 (282)	10 ± 0.1 (31)	7 ± 0.1 (30)	69	31
awru1-B-06	Davis	NA	NA	3/03/2007	186	17 ± 0.1 (24)	4 ± 0.2 (16)	10 ± 0.1 (16)	3295	18 ± 0.7 (55)	109 ± 1 (242)	14 ± 0.1 (55)	8 ± 0.1 (50)	22	78
	DDU	**230 ± 3**	**284 ± 17**		**180 ± 13 (242)**	**32 ± 0.2 (259)**	**4 ± 1 (75)**	**9 ± 0.1 (98)**	**30319**	**15 ± 0.9 (82)**	**115 ± 0.6 (904)**	**12 ± 0.03 (84)**	**7 ± 0.03 (76)**	**34 ± 6 (75)**	**66 ± 6 (91)**
	Davis	**240 ± 3**	**365 ± 13**		**158 ± 7 (199)**	**99 ± 0.3 (372)**	**11 ± 1 (144)**	**32 ± 0.2 (293)**	**50170**	**18 ± 0.9 (81)**	**179 ± 0.6 (1094)**	**13 ± 0.03 (84)**	**6 ± 0.02 (69)**	**29 ± 3 (69)**	**71 ± 3 (89)**
	wilcoxon test DDU vs Davis					W = 195, p-value < 0.05	W = 207, p-value < 0.001	W = 205, p-value < 0.05			W = 193, p-value < 0.05	W = 165, p-value < 0.05	W = 52, p-value = 0.1		

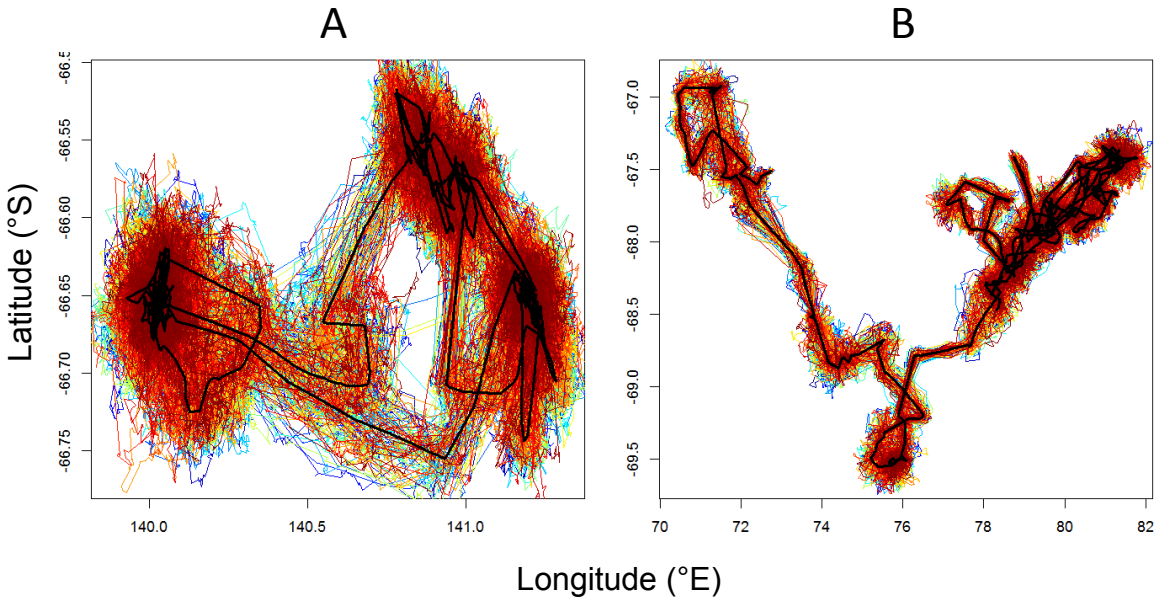

Figure S5.1. Examples of the argos tracks filtered with a correlated random walk mode (CRWM) for one Weddell seal from DDU (A) and Davis (B). Locations were interpolated at each dive time for the main track (black line) and 100 simulated tracks using the CRWM.

Table S5.2. Summary of area-restricted search metrics obtained from First-Passage Time (FPT) and First-Hunting Time (FHT) analysis. The FHT values were calculated for each dive at the FHT optimal scale for each individual. FHT threshold used to discriminate hunting from transit mode was calculated as described in the methods section 3.5.2. Transit: FHT values ≤ FHT threshold; hunting: FHT values > FHT threshold. Wilcoxon tests were used to compare FHT metrics between Dumont D'Urville and Davis. Most of the individuals were adult females, although the ID of males is coloured in blue.

Seal ID	Colony	Optimal scale of FPT (km)	Optimal scale of FHT (km)	FHT (hour)	Threshold of FHT: hunting vs transit (hour)	% of dives in hunting mode	% of dives in transit mode
wd3-CTD2-07	DDU	3.6	3.6	8 ± 0.2 (47)	3.8	57	43
wd3-CTD1-07	DDU	3	3.4	34 ± 0.7 (115)	8.05	72	28
wd3-CTD3-07	DDU	1.4	4.8	16 ± 0.3 (50)	6.7	58	42
ct38w-QueenEliz-08	DDU	1.4	6	22 ± 0.3 (57)	15.67	49	51
ct38w-Denise-08	DDU	1.2	3.4	35 ± 0.7 (88)	12.27	65	35
ct38w-Mathilde-08	DDU	1.8	6.5	27 ± 0.6 (93)	9.82	63	37
ct47-B-09	DDU	3	15	17 ± 0.4 (50)	6.88	61	39
ct47-G-09	DDU	6.5	3.2	24 ± 0.5 (69)	12.57	42	58
ct47-C-09	DDU	2.2	5.5	5 ± 0.1 (19)	3.14	56	44
ct47-I-09	DDU	0.5	0.5	3 ± 0.06 (10)	3.84	27	73
ct47-D-09	DDU	3.2	1.4	1 ± 0.03 (5)	0.78	44	55
ct47-A-09	DDU	1.8	7	62 ± 1 (153)	45.11	44	56
wd04-880-11	Davis	2.4	0.7	0.8 ± 0.02 (5)	0.51	44	43
wd04-838-11	Davis	3	12.5	9 ± 0.2 (28)	3.15	69	31
wd04-910-11	Davis	6	5.5	15 ± 0.6 (75)	3.13	55	45
wd04-884-11	Davis	15	0.5	0.4 ± 0.01 (3)	0.27	33	39
wd04-883-11	Davis	3.4	0.5	0.6 ± 0.01 (4)	0.43	31	47
wd04-897-11	Davis	15	15	7.3 ± 0.2 (40)	3.02	60	40
wd04-909-11	Davis	4.4	4.6	2 ± 0.05 (15)	1.34	43	57
wd04-907-11	Davis	4.8	14.5	13 ± 0.4 (62)	5.14	41	59
wd04-896-11	Davis	3.2	0.7	0.4 ± 0.01 (4)	0.38	29	55

wd04-906-11	Davis	1.2	1.2	0.8 ± 0.02 (4)	0.61	44	55
wd04-836-11	Davis	2.4	0.5	0.5 ± 0.1 (3)	0.38	33	41
wd04-898-11	Davis	1	1	4 ± 0.07 (19)	3.38	40	60
wd04-908-11	Davis	4.4	0.5	0.4 ± 0.1 (2)	0.25	39	32
wd04-900-11	Davis	6	0.5	0.4 ± 0.01 (3)	0.2	36	31
wd04-881-11	Davis	1.4	1.4	0.9 ± 0.03 (4)	0.63	47	48
wd1-10213-06	Davis	9	9	8 ± 0.2 (43)	4.56	40	60
wd1-10183-06	Davis	1.2	1.2	1.9 ± 0.06 (10)	1.03	59	40
awru1-A-06	Davis	8.5	10	14 ± 0.2 (41)	9.78	50	50
awru1-C-06	Davis	0.7	5.5	23 ± 0.4 (75)	6.49	78	22
awru1-B-06	Davis	5	6.5	54 ± 0.9 (216)	32	46	54
	DDU	2.5 ± 0.5 (6.5)	5 ± 1 (15)	24 ± 0.2 (153)	11 ± 3 (45)	53 ± 4 (72)	47 ± 3 (73)
	Davis	4.9 ± 0.9 (15)	4.6 ± 1 (15)	10 ± 0.1 (216)	4 ± 2 (32)	46 ± 3 (78)	45 ± 2 (60)
	wilcoxon test DDU vs Davis		w = 95, p-value = 0.34	**W = 44, p-value < 0.05**	**W = 38, p-value < 0.05**	w = 75, p-value = 0.08	w = 120, p-value = 1

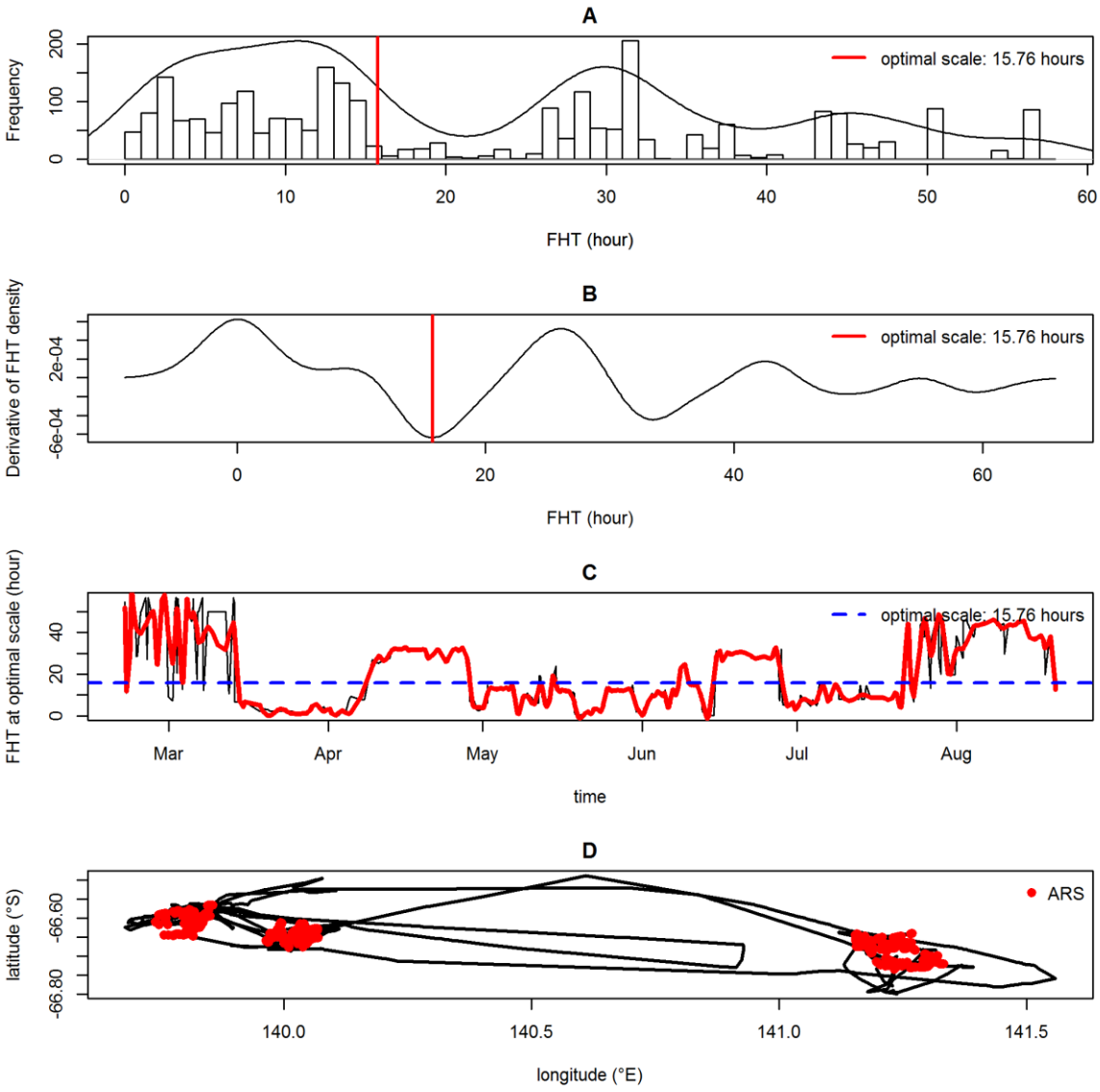

Figure S5.2. Plots of the distribution of First-Hunting Time (FHT) values and their density (A), the derivative of FHT values' density (B), the temporal evolution of FHT values (C) and a map representing the track of one individual (D).

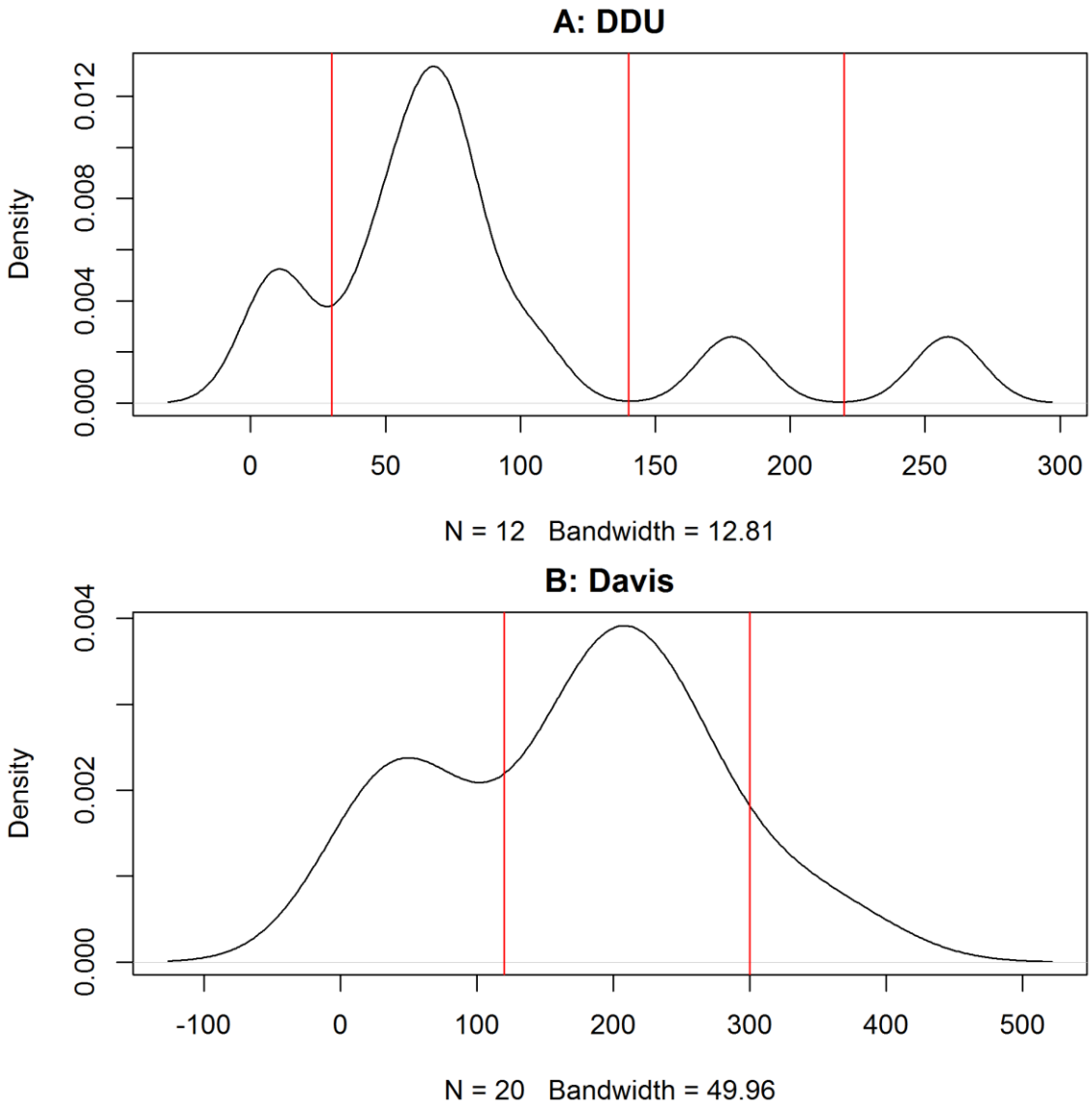

Figure S5.3. Density distributions of maximum distances travelled from deployment site for each individual in Dumont D'Urville (A) and Davis (B). The vertical redlines indicate inflexion points in the density curve which were used to discriminate the different maximum distance classes (See Fig.5.7 and 5.8).

Table S5.3. Summary of diving behaviour metrics when an individual exhibits hunting and transit modes. Values are presented as mean ± se (max). Wilcoxon tests were used to compare diving metrics: (i) between behavioural modes within each colony and (ii) of each behavioural mode between colonies. Most of the individuals were adult females, although the ID of males is coloured in blue.

Seal ID	Colony	Maximal dive depth (m)		Dive duration (min)		Hunting time (min)	
		Hunting	*Transit*	*Hunting*	*Transit*	*Hunting*	*Transit*
wd3-CTD2-07	DDU	154 ± 2 (416)	153 ± 2 (574)	12 ± 0.1 (38)	11 ± 0.1 (32)	8 ± 0.1 (32)	6 ± 0.1 (27)
wd3-CTD1-07	DDU	75 ± 1 (301)	86 ± 2 (431)	13 ± 0.1 (29)	13 ± 0.2 (38)	9 ± 0.1 (27)	8 ± 0.2 (30)
wd3-CTD3-07	DDU	127 ± 5 (371)	172 ± 5 (684)	11 ± 0.3 (33)	10 ± 0.2 (25)	7 ± 0.2 (26)	5 ± 0.2 (19)
ct38w-QueenEliz-08	DDU	68 ± 1 (321)	83 ± 2 (456)	10 ± 0.1 (29)	11 ± 0.1 (36)	7 ± 0.1 (21)	7 ± 0.1 (30)
ct38w-Denise-08	DDU	73 ± 1 (196)	95 ± 2 (316)	13 ± 0.2 (31)	13 ± 0.2 (31)	8 ± 0.2 (25)	8 ± 0.2 (25)
ct38w-Mathilde-08	DDU	89 ± 1 (241)	87 ± 3 (461)	12 ± 0.2 (84)	12 ± 0.2 (38)	9 ± 0.2 (76)	8 ± 0.2 (29)
ct47-B-09	DDU	53 ± 2 (196)	106 ± 5 (554)	9 ± 0.2 (26)	10 ± 0.3 (26)	6 ± 0.2 (22)	5 ± 0.2 (18)
ct47-G-09	DDU	58 ± 1 (118)	64 ± 1 (221)	8 ± 0.1 (17)	8 ± 0.1 (23)	5 ± 0.1 (15)	5 ± 0.1 (18)
ct47-C-09	DDU	65 ± 2 (311)	98 ± 5 (401)	11 ± 0.3 (35)	10 ± 0.3 (26)	7 ± 0.2 (30)	6 ± 0.3 (20)
ct47-I-09	DDU	59 ± 1 (123)	58 ± 1 (145)	11 ± 0.2 (26)	10 ± 0.2 (24)	8 ± 0.2 (23)	7 ± 0.2 (21)
ct47-D-09	DDU	120 ± 2 (376)	122 ± 3 (396)	11 ± 0.2 (53)	10 ± 0.2 (27)	7 ± 0.2 (46)	5 ± 0.1 (22)
ct47-A-09	DDU	70 ± 1 (201)	74 ± 1 (441)	11 ± 0.1 (32)	9 ± 0.2 (32)	8 ± 0.1 (24)	6 ± 0.1 (21)
wd04-880-11	Davis	251 ± 5 (514)	205 ± 4 (564)	16 ± 0.2 (45)	12 ± 0.2 (33)	7.8 ± 0.1 (35)	5 ± 0.1 (24)
wd04-838-11	Davis	126 ± 2 (381)	132 ± 5 (431)	10 ± 0.2 (31)	10 ± 0.3 (29)	5 ± 0.1 (25)	5 ± 0.2 (21)
wd04-910-11	Davis	185 ± 5 (564)	187 ± 6 (604)	16 ± 0.3 (62)	12 ± 0.3 (35)	8 ± 0.2 (52)	4 ± 0.2 (31)
wd04-884-11	Davis	216 ± 8 (624)	141 ± 6 (644)	14 ± 0.3 (33)	9 ± 0.2 (28)	7 ± 0.2 (25)	3 ± 0.1 (14)
wd04-883-11	Davis	178 ± 4 (594)	190 ± 4 (584)	14 ± 0.2 (37)	11 ± 0.1 (41)	8 ± 0.2 (35)	4 ± 0.1 (23)
wd04-897-11	Davis	159 ± 4 (604)	140 ± 4 (634)	13 ± 0.2 (49)	12 ± 0.1 (42)	6 ± 0.1 (29)	5 ± 0.1 (25)
wd04-909-11	Davis	211 ± 4 (714)	264 ± 4 (774)	15 ± 0.2 (68)	17 ± 0.2 (65)	6 ± 0.2 (46)	5 ± 0.1 (44)
wd04-907-11	Davis	157 ± 4 (476)	184 ± 5 (544)	14 ± 0.3 (39)	11 ± 0.2 (41)	7 ± 0.3 (35)	3 ± 0.1 (28)
wd04-896-11	Davis	151 ± 5 (664)	153 ± 4 (704)	9 ± 0.3 (45)	9 ± 0.1 (28)	5 ± 0.2 (36)	3 ± 0.1 (21)
wd04-906-11	Davis	111 ± 4 (346)	99 ± 3 (281)	13 ± 0.3 (56)	7 ± 0.2 (28)	7 ± 0.2 (47)	3 ± 0.1 (22)

wd04-836-11	Davis	169 ± 3 (554)	150 ± 3 (533)	12 ± 0.2 (49)	9 ± 0.1 (29)	6 ± 0.2 (49)	3 ± 0.1 (20)
wd04-898-11	Davis	84 ± 1 (171)	85 ± 1 (216)	11 ± 0.1 (28)	11 ± 0.1 (35)	8 ± 0.1 (28)	8 ± 0.1 (35)
wd04-908-11	Davis	170 ± 5 (534)	133 ± 5 (574)	14 ± 0.3 (43)	10 ± 0.2 (25)	7 ± 0.2 (37)	3 ± 0.1 (14)
wd04-900-11	Davis	232 ± 5 (554)	166 ± 5 (764)	14 ± 0.2 (39)	10 ± 0.2 (27)	6 ± 0.2 (30)	2 ± 0.1 (12)
wd04-881-11	Davis	171 ± 5 (411)	189 ± 6 (534)	13 ± 0.3 (33)	11 ± 0.3 (33)	7 ± 0.3 (30)	4 ± 0.2 (25)
wd1-10213-06	Davis	132 ± 3 (581)	212 ± 3 (875)	10 ± 0.2 (58)	13 ± 0.1 (39)	4 ± 0.1 (45)	4 ± 0.1 (28)
wd1-10183-06	Davis	112 ± 3 (218)	104 ± 3 (212)	12 ± 0.3 (31)	9 ± 0.3 (29)	7 ± 0.2 (21)	4 ± 0.2 (23)
awru1-A-06	Davis	121 ± 1 (234)	101 ± 2 (258)	11 ± 0.1 (30)	11 ± 0.1 (31)	5 ± 0.1 (23)	5 ± 0.1 (28)
awru1-C-06	Davis	66 ± 0.5 (146)	63 ± 1 (202)	10 ± 0.1 (31)	10 ± 0.2 (30)	7 ± 0.1 (30)	7 ± 0.2 (26)
awru1-B-06	Davis	116 ± 1 (226)	105 ± 1 (242)	15 ± 0.2 (53)	12 ± 0.1 (55)	9 ± 0.2 (50)	7 ± 0.1 (46)
	DDU	84 ± 9 (376)	100 ± 10 (684)	11 ± 0.5 (84)	11 ± 0.4 (53)	8 ± 0.4 (76)	6 ± 0.4 (30)
	Davis	156 ± 11 (376)	150 ± 11 (875)	13 ± 0.5 (68)	11 ± 0.4 (65)	7 ± 0.3 (52)	4 ± 0.3 (46)
	DDU	w=49 , p= 0.19		w=88 , p= 0.38		**W=108, p<0.05**	
	Davis	w=214, p= 0.72		**w=307, p<0.05**		**W=343, p<0.001**	
	DDU vs Davis	**w=213, p < 0.001**	**w=192, p<0.05**	**w=176, p<0.05**	w=117, p=0.92	**w=178, p<0.05**	**w=206, p<0.001**

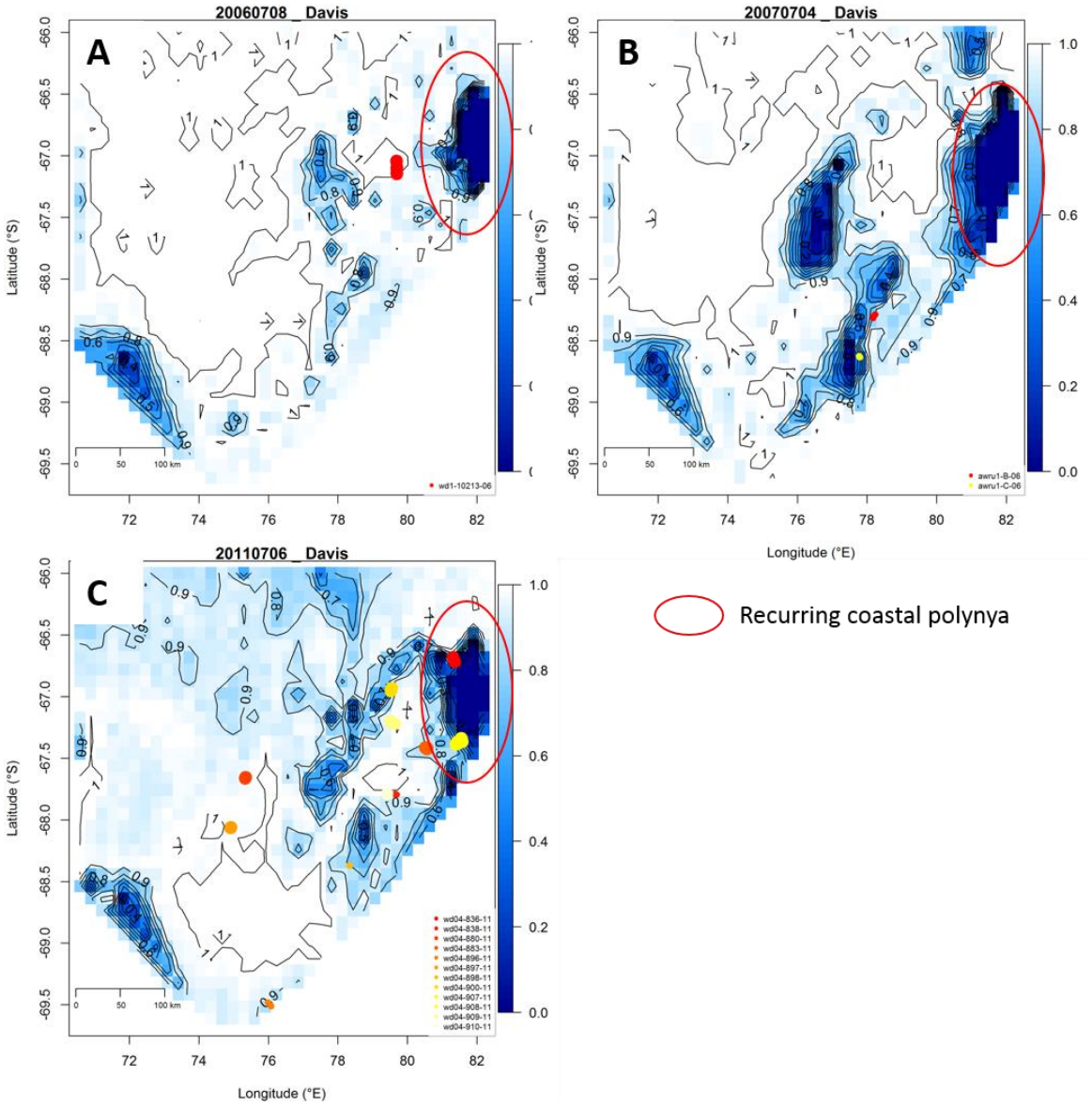

Figure S5.4. Daily maps of sea-ice concentration obtained from the AMSRE satellile for the Davis site. It shows the existence of a recurring small coastal polynya on a pluri-annual basis (2006: A, 2007: B, 2011: C) in winter (beginning of july for the images presented).

Table S5.4. Summary of environmental variables associated with each behavioural mode (i.e. hunting or transit) for each individual. Values are presented as mean ± se (max). Wilcoxon tests were used to compare diving metrics: (i) between behavioural modes within each colony and (ii) of each behavioural mode between colonies. Most of the individuals were adult females, although the ID of males is coloured in blue.

Seal ID	Colony	Bathymetry (m)		Slope (degree)		Sea-ice concentration		Sd of sea-ice concentration in 25 km		distance to sea-ice edge (km)	
		Hunting	*Transit*	*Hunting*	*Transit*	*Hunting*	*Transit*	*Hunting*	*Transit*	*Hunting*	*Transit*
wd3-CTD2-07	DDU	242 ± 2 (491)	239 ± 3 (1062)	4 ± 0.1 (15)	4 ± 0.1 (16)	0.7 ± 0.01 (1)	0.7 ± 0.01 (1)	0.08 ± 0.003 (0.4)	0.1 ± 0.002 (0.4)	43 ± 1 (138)	43 ± 1 (149)
wd3-CTD1-07	DDU	211 ± 2 (560)	277 ± 6 (982)	7 ± 0.1 (14)	9 ± 0.1 (18)	0.7 ± 0.01 (1)	0.5 ± 0.01 (1)	0.1 ± 0.002 (0.4)	0.1 ± 0.004 (0.4)	49 ± 1 (191)	31 ± 1 (183)
wd3-CTD3-07	DDU	194 ± 3 (386)	439 ± 8 (810)	3 ± 0.08 (11)	2 ± 0.05 (10)	0.7 ± 0.01 (1)	0.9 ± 0.01 (1)	0.09 ± 0.003 (0.4)	0.1 ± 0.004 (0.4)	50 ± 1 (141)	61 ± 1 (165)
ct38w-QueenEliz-08	DDU	176 ± 2 (425)	251 ± 4 (861)	7 ± 0.05 (12)	7 ± 0.1 (17)	0.6 ± 0.02 (1)	0.8 ± 0.01 (1)	0.05 ± 0.002 (0.3)	0.1 ± 0.004 (0.4)	58 ± 2 (141)	79 ± 2 (219)
ct38w-Denise-08	DDU	235 ± 6 (845)	235 ± 6 (845)	6 ± 0.2 (16)	6 ± 0.2 (16)	0.9 ± 0.01 (1)	0.9 ± 0.01 (1)	0.07 ± 0.004 (0.4)	0.07 ± 0.004 (0.4)	66 ± 1 (114)	66 ± 1 (114)
ct38w-Mathilde-08	DDU	143 ± 2 (390)	200 ± 5 (919)	5 ± 0.1 (12)	7 ± 0.1 (17)	0.7 ± 0.01 (1)	0.6 ± 0.01 (1)	0.09 ± 0.003 (0.4)	0.1 ± 0.004 (0.4)	54 ± 1 (181)	43 ± 2 (180)
ct47-B-09	DDU	98 ± 3 (301)	297 ± 13 (1180)	3 ± 0.03 (6)	2 ± 0.1 (6)	0.6 ± 0.02 (1)	0.9 ± 0.01 (1)	0.2 ± 0.005 (0.4)	0.09 ± 0.006 (0.4)	40 ± 2 (152)	88 ± 4 (318)
ct47-G-09	DDU	85 ± 1 (185)	114 ± 1 (246)	5 ± 0.02 (7)	6 ± 0.04 (12)	0.5 ± 0.01 (1)	0.5 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.1 ± 0.003 (0.4)	32 ± 2 (162)	32 ± 1 (133)
ct47-C-09	DDU	154 ± 4 (405)	310 ± 10 (852)	6 ± 0.09 (11)	7 ± 0.1 (14)	0.5 ± 0.02 (1)	0.8 ± 0.01 (1)	0.2 ± 0.005 (0.4)	0.1 ± 0.005 (0.4)	32 ± 2 (162)	73 ± 3 (171)
ct47-I-09	DDU	58 ± 2 (157)	68 ± 1 (162)	5 ± 0.06 (9)	5 ± 0.04 (9)	0.5 ± 0.02 (1)	0.6 ± 0.01 (1)	0.1 ± 0.006 (0.3)	0.2 ± 0.004 (0.4)	32 ± 3 (163)	38 ± 1 (163)
ct47-D-09	DDU	209 ± 4 (663)	243 ± 5 (680)	5 ± 0.1 (15)	5 ± 0.1 (14)	0.4 ± 0.02 (1)	0.4 ± 0.01 (1)	0.1 ± 0.01 (0.4)	0.2 ± 0.004 (0.4)	26 ± 1 (118)	28 ± 1 (159)
ct47-A-09	DDU	191 ± 3 (852)	222 ± 5 (1184)	7 ± 0.1 (17)	8 ± 0.1 (18)	0.6 ± 0.01 (1)	0.8 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.1 ± 0.003 (0.3)	35 ± 1 (155)	66 ± 1 (171)
wd04-880-11	Davis	545 ± 18 (2804)	587 ± 20 (2950)	1 ± 0.04 (9)	1 ± 0.05 (10)	0.9 ± 0.005 (1)	0.9 ± 0.01 (1)	0.1 ± 0.002 (0.3)	0.1 ± 0.003 (0.3)	108 ± 2 (285)	96 ± 2 (285)
wd04-838-11	Davis	278 ± 3 (616)	348 ± 7 (645)	1 ± 0.02 (6)	1 ± 0.02 (3)	0.7 ± 0.01 (1)	0.7 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.2 ± 0.005 (0.4)	39 ± 2 (218)	37 ± 2 (211)
wd04-910-11	Davis	350 ± 4 (662)	384 ± 5 (677)	1 ± 0.03 (9)	1 ± 0.02 (4)	0.9 ± 0.01 (1)	0.9 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.1 ± 0.004 (0.4)	38 ± 1 (134)	50 ± 2 (177)
wd04-884-11	Davis	353 ± 9 (895)	397 ± 9 (848)	1 ± 0.07 (9)	1 ± 0.06 (9)	0.8 ± 0.01 (1)	0.8 ± 0.01 (1)	0.1 ± 0.007 (0.4)	0.1 ± 0.006 (0.4)	68 ± 3 (373)	74 ± 3 (373)
wd04-883-11	Davis	332 ± 6 (997)	411 ± 5 (980)	1 ± 0.04 (10)	1 ± 0.03 (8)	0.6 ± 0.01 (1)	0.7 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.2 ± 0.003 (0.4)	22 ± 1 (123)	37 ± 1 (143)

wd04-897-11	Davis	365 ± 5 (823)	445 ± 5 (823)	0.9 ± 0.01 (8)	0.8 ± 0.02 (5)	0.8 ± 0.01 (1)	0.9 ± 0.01 (1)	0.1 ± 0.003 (0.3)	0.1 ± 0.003 (0.3)	66 ± 2 (257)	79 ± 2 (282)
wd04-909-11	Davis	502 ± 5 (804)	496 ± 4 (997)	2 ± 0.01 (4)	2 ± 0.02 (4)	0.9 ± 0.01 (1)	0.8 ± 0.01 (1)	0.1 ± 0.002 (0.4)	0.1 ± 0.002 (0.5)	44 ± 1 (150)	46 ± 1 (151)
wd04-907-11	Davis	211 ± 4 (571)	374 ± 5 (643)	1 ± 0.03 (6)	1 ± 0.04 (11)	0.7 ± 0.01 (1)	0.7 ± 0.01 (1)	0.3 ± 0.004 (0.5)	0.2 ± 0.004 (0.5)	16 ± 1 (90)	34 ± 1 (132)
wd04-896-11	Davis	200 ± 4 (398)	351 ± 5 (808)	1 ± 0.02 (3)	1 ± 0.02 (9)	0.8 ± 0.03 (1)	0.8 ± 0.01 (1)	0.2 ± 0.004 (0.4)	0.2 ± 0.003 (0.4)	46 ± 3 (396)	55 ± 2 (405)
wd04-906-11	Davis	316 ± 6 (695)	199 ± 3 (409)	2 ± 0.02 (4)	1 ± 0.04 (7)	0.7 ± 0.01 (1)	0.8 ± 0.01 (1)	0.2 ± 0.004 (0.4)	0.2 ± 0.004 (0.4)	37 ± 1 (132)	52 ± 2 (196)
wd04-836-11	Davis	413 ± 5 (718)	400 ± 5 (751)	1 ± 0.02 (7)	1 ± 0.02 (7)	0.8 ± 0.01 (1)	0.8 ± 0.01 (1)	0.1 ± 0.003 (0.5)	0.2 ± 0.003 (0.5)	39 ± 1 (135)	39 ± 1 (143)
wd04-898-11	Davis	156 ± 2 (283)	168 ± 2 (531)	1 ± 0.02 (5)	1 ± 0.02 (8)	0.8 ± 0.005 (1)	0.8 ± 0.004 (1)	0.2 ± 0.002 (0.4)	0.2 ± 0.002 (0.4)	53 ± 2 (269)	50 ± 1 (270)
wd04-908-11	Davis	394 ± 6 (652)	400 ± 6 (639)	0.8 ± 0.02 (2)	0.9 ± 0.03 (5)	0.9 ± 0.005 (1)	0.9 ± 0.006 (1)	0.1 ± 0.004 (0.4)	0.1 ± 0.004 (0.3)	97 ± 2 (297)	96 ± 3 (297)
wd04-900-11	Davis	440 ± 5 (881)	438 ± 8 (1072)	2 ± 0.02 (3)	1 ± 0.02 (3)	0.8 ± 0.01 (1)	0.8 ± 0.01 (1)	0.1 ± 0.004 (0.5)	0.2 ± 0.004 (0.5)	40 ± 1 (185)	33 ± 1 (185)
wd04-881-11	Davis	282 ± 6 (527)	363 ± 6 (597)	2 ± 0.02 (3)	2 ± 0.03 (7)	0.8 ± 0.01 (1)	0.8 ± 0.01 (1)	0.2 ± 0.004 (0.3)	0.1 ± 0.005 (0.4)	27 ± 1 (148)	50 ± 2 (139)
wd1-10213-06	Davis	388 ± 7 (1094)	663 ± 5 (1126)	3 ± 0.07 (16)	2 ± 0.02 (7)	0.8 ± 0.005 (1)	0.8 ± 0.005 (1)	0.1 ± 0.002 (0.4)	0.1 ± 0.002 (0.3)	34 ± 0.6 (92)	39 ± 0.5 (110)
wd1-10183-06	Davis	175 ± 2 (270)	191 ± 3 (302)	2 ± 0.06 (7)	1 ± 0.04 (6)	0.7 ± 0.01 (1)	0.8 ± 0.01 (1)	0.2 ± 0.003 (0.3)	0.2 ± 0.004 (0.3)	34 ± 2 (154)	38 ± 2 (177)
awru1-A-06	Davis	182 ± 1 (280)	212 ± 2 (304)	1 ± 0.02 (6)	1 ± 0.03 (11)	0.8 ± 0.01 (1)	0.5 ± 0.01 (1)	0.2 ± 0.003 (0.4)	0.3 ± 0.002 (0.4)	35 ± 1 (214)	12 ± 0.4 (126)
awru1-C-06	Davis	111 ± 2 (291)	145 ± 4 (544)	2 ± 0.02 (11)	2± 0.07 (10)	0.5 ± 0.01 (1)	0.4 ± 0.02 (1)	0.3 ± 0.007 (0.4)	0.3 ± 0.003 (0.4)	31 ± 1 (239)	9 ± 0.5 (55)
awru1-B-06	Davis	195 ± 1 (295)	225 ± 1 (303)	1 ± 0.02 (10)	1 ± 0.03 (12)	0.8 ± 0.01 (1)	0.6 ± 0.01 (1)	0.2 ± 0.002 (0.4)	0.2 ± 0.002 (0.4)	40 ± 1 (207)	23 ± 1 (205)
	DDU	158 ± 16 (852)	241 ± 27 (1184)	5 ± 0.4 (17)	6 ± 0.6 (18)	0.6 ± 0.03 (1)	0.7 ± 0.05 (1)	0.1 ± 0.02 (0.4)	0.1 ± 0.01 (0.4)	42 ± 3 (191)	54 ± 6 (318)
	Davis	309 ± 27 (2804)	360 ± 31 (2950)	1 ± 0.1 (16)	1 ± 0.1 (12)	0.8 ± 0.02 (1)	0.7 ± 0.03 (1)	0.2 ± 0.01 (0.5)	0.2 ± 0.01 (0.5)	46 ± 5 (396)	47 ± 5 (405)
	DDU	**W=118, p<0.05**		w=80, p=0.67		w=101, p=0.10		w=73, p=0.98		w=94, p=0.11	
	Davis	W=247, p=0.11		w=187, p=0.74		w=201, p=0.99		w=179, p=0.58		w=217, p=0.33	
	DDU vs Davis	**w=207, p<0.001**	**w=173, p<0.05**	**w=239, p<0.001**	**w=238, p<0.001**	**w=219, p<0.001**	w=99, p=0.43	**w=175, p<0.05**	**w=174, p<0.05**	w=124, p=0.89	w=104, p=0.55

Table S 5.5. Generalized mixed effect model output for the final model (on dives from both colonies) including each significant fixed explanatory variables. ARS is the binomial response variable: "transit" or "hunting". DDU and DOY stand for Dumont d'Urville and day of year, respectively. The colony was used as a factor and its interaction with the bathymetry and the day of year was significant. Individuals were used as random effect on the intercept.

Model: ARS ~ bathymetry + DOY + as.factor(colony) + as.factor(colony) * DOY + as.factor(colony) * bathymetry

n observations: 18666

n individuals: 32

Random effects: ~1 | seal ID

	(Intercept)	Residual
StdDev:	0.5085548	0.9785015

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.4049332	0.1395441	18630	2.90183	0.00370
Bathymetry	-0.0013331	0.00019183	18630	-6.94942	0.00000
DOY	0.5769622	0.05639448	18630	10.230827	0.00000
as.factor(colony)DDU	0.2045541	0.22302438	30	0.917183	0.36640
DOY:as.factor(colony)DDU	-0.5780907	0.08560738	18630	-6.752813	0.00000
Bathymetry:as.factor(colony)DDU	-0.0014093	0.00036167	18630	-3.896693	0.00010

Table S5.6. Generalized mixed effect model output for the final model (on dives from Dumont D'Urville) including each significant fixed explanatory variables. ARS is the binomial response variable: "transit" or "hunting". DOY stands for day of year. Dist_ie is the distance to low ice concentrations ([sea-ice] ≤ 0.2). The year was used as a factor and its interaction with the bathymetry and the day of year was significant. Individuals were used as random effect on the intercept.

Model: ARS ~ bathymetry + dist_ie + DOY + as.factor(year) + as.factor(year) * bathymetry + as.factor(year) * DOY

n observations: 19812

n individuals: 12

Random effects: ~1 | Seal ID

	(Intercept)	Residual
StdDev:	0.001620159	1.045573

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.8585424	0.1907336	19793	4.501265	0.00000
mean_bath	-0.0008979	0.00032054	19793	-2.801366	0.00510
dist_ie	-0.0624792	0.02546119	19793	-2.453899	0.01410
day	0.9589843	0.14042582	19793	6.829117	0.00000
as.factor(year)2008	-0.465057	0.26099977	9	-1.781829	0.10850
as.factor(year)2009	-1.2039723	0.24557528	9	-4.902661	0.00080
mean_bath:as.factor(year)2008	-0.0002491	0.00043202	19793	-0.576663	0.56420
mean_bath:as.factor(year)2009	-0.0021013	0.00043248	19793	-4.858614	0.00000
day:as.factor(year)2008	-0.8002663	0.16821846	19793	-4.757304	0.00000
day:as.factor(year)2009	-1.9716347	0.18008758	19793	-10.9482	0.00000

Table S5.7. Generalized mixed effect model output for the final model (on dives from Davis) including each significant fixed explanatory variables. ARS is the binomial response variable: "transit" or "hunting". DOY stands for day of year. Sdice 25 is the variation of sea-ice concentration within 25 km around each dive. The year was used as a factor and its interaction with the bathymetry and the day of year was significant. Individuals were used as random effect on the intercept.

Model: ARS ~ bathymetry + sdice25 + DOY + as.factor(year) + as.factor(year) * bathymetry

n observations: 18991

n individuals: 20

Random effects: ~1 | seal ID

	(Intercept)	Residual
StdDev:	0.4460315	0.9853323

	Value	Std.Error	DF	t-value	p-value
(Intercept)	1.0320515	0.3908709	18966	2.64039	0.00830
Bathymetry	-0.0033658	0.0004679	18966	-7.193555	0.00000
sdice25	-0.0787766	0.0320467	18966	-2.458184	0.01400
DOY	0.584068	0.0503898	18966	11.590986	0.00000
as.factor(year)2007	0.1916197	0.5073647	17	0.377677	0.71030
as.factor(year)2011	-0.7457441	0.4167614	17	-1.789379	0.09140
Bathymetry:as.factor(year)2007	-0.0007908	0.0010475	18966	-0.754918	0.45030
Bathymetry:as.factor(year)2011	0.002265	0.0005092	18966	4.447863	0.00000

D - Conclusion

These two chapters were complementary by considering different aspect of Weddell seal foraging behaviour in relation to their winter environment. The first chapter considered the vertical use of the water column (*i.e.* diving behaviour) while the second integrated within dive foraging effort to identifies areas associated with ARS behaviour in the three dimensions (temporal, horizontal and vertical) (*i.e.* Foraging habitat use). **They both revealed the significant influence of some temporal and abiotic features on Weddell seal's diving behaviour and habitat use in East Antarctica.**

These two studies showed some differences and similarities in the habitat use of the Weddell seals from both sites. Weddell seals from Davis essentially travelled more and their foraging activity was more dispersed than the seals from DDU that showed a strong residency to the same areas. The two sites also differed in their environmental conditions (*e.g.* sea-ice, topography) which can be a reason for the difference observed in movement and foraging patterns. However, overall, at both sites, Weddell seals remained in the coastal area covered with fast-ice and essentially used shallow areas. Indeed, the topography was clearly important to the Weddell seal habitat use as they concentrated their foraging effort and adapted their diving behaviour according to the bathymetry. The bathymetric slope influenced diving behaviour and foraging effort at the dive scale while it did not influence the switch toward hunting mode at the optimal foraging scale. The two studies also brought complementary results about the influence of winter advance on the foraging and diving behaviour of Weddell seals from East-Antarctica. Paper 4 showed seals dived shallower and longer without an increase of foraging effort (estimated from bottom time residuals) with winter advance. The analyses of Paper 5 demonstrated a higher

probability of switching to ARS behaviour but without an increase of the time spent hunting within a dive (estimated from reduced vertical velocity segments) (results not presented in Paper 5). In combination, these results suggest that with winter advance Weddell seals do not change their within dive foraging effort but instead intensify their foraging effort within a given area around a breathing hole or several ones in close distance to each other (optimal ARS scale of ~4-5 km see Paper 5). Although sea-ice concentrations did not directly influence Weddell seals' behavioural response (Paper 4 and 5), other derived sea-ice metrics were related to their foraging activity (Paper 5). Our studies suggested Weddell seals used highly concentrated ice but in areas where sea-ice is thinner (*e.g.* proximity with open water areas) and/or where physical forcing are likely to facilitate the persistence of cracks (*e.g.* proximity of land and shallow bathymetry) needed by the seals to breathe. Weddell seals also adapted their diving behaviour to the time of the day, with pelagic and shallower dives being essentially performed at night while diving deeper and benthically during the day. This suggest that seals are likely following the diurnal migration of their prey but also that they likely need light intensity to orientate themselves and pursue their prey. The influence of water masses on Weddell seal diving behaviour was investigated in Paper 4 but could not be integrated in Paper 5. Indeed, for the Davis seals temperature profiles were collected but not conductivity which is necessary to discriminate the different water masses. At DDU, the Weddell seals tended to target and forage in enriched, warmer and less dense water masses following their seasonal appearance on the shelf (AASW and then MCDW).

Overall, our results suggested Weddell seals optimize foraging during winter by selecting habitat likely associated with better prey availability and accessibility as well as areas facilitating breathing holes upkeep. Our results were also concordant with Weddell seals foraging primarly on *Pleurogramma antarctium.*

However, seals also showed some behavioural plasticity (*i.e.* foraging areas, diving depths) suggesting they can switch habitat use and diet according to prey availability and accessibility as well as physiological constraints (*i.e.* need to breathe in the fast-ice environment).

PART IV

GENERAL DISCUSSION, CONCLUSIONS AND PERSPECTIVES

Dessin de Coralie Chorin – photo Karine Heerah

A - Methodological discussion

The main objective of this PhD was to improve our understanding of how Weddell seals optimize their foraging strategies during winter in relation to the environment. This relied on our ability to identify and quantify foraging effort and to relate the seals' foraging behaviour to appropriate environmental features at appropriate spatial and temporal scales. However, the simplicity and resolution of the datasets available for this study raised several methodological challenges that will be discussed below.

1. Analysis of diving behaviour to infer foraging activity

1.1 The development of a new method

The first constraint of our dataset was the absence of concurrent information on prey encounters and feeding events which required to develop and use proxies of foraging activity in our ecological analysis. Moreover, we only had access to Time-depth data, including only a high-resolution dive dataset collected by one individual and a large low-resolution dive dataset collected by several individuals. It was therefore necessary to develop a method that detects within-dive intensive foraging behaviour and quantify dive foraging effort using both high and low-resolution dive datasets. The method, termed "Hunting Method", relies on the transposition of the ARS definition into the vertical dimension, and uses the premise that a diving predator would increase its time in a patch of prey by increasing the vertical sinuosity of its trajectory and decreasing its vertical speed

at depths of interest. The fundamental advantage of this approach over other methods is that it detects foraging activity along the whole dive profile rather than assuming foraging to occur exclusively in limited parts of a dive (such as the bottom time).

1.1.1 Advantages of the "hunting method"

The main advantage of this method is that it should be applicable to any diving species for which foraging is associated with vertical ARS behaviour. Indeed, vertical ARS behaviour, quantified using "wiggles" within a dive profile, has already been associated with prey capture for seals, penguins and whales (Simeone & Wilson 2003; Goldbogen *et al.* 2006; Bost *et al.* 2007; Calambokidis *et al.* 2007; Hanuise *et al.* 2010; Watanabe & Takahashi 2013a). The threshold set for the SES and the Weddell seals in this thesis may not necessarily be appropriate for other species. However, one could easily find a suitable threshold (to discriminate "transit" from "hunting" behaviour) for a given species by looking at the distribution of the vertical sinuosity (if working with high resolution dive profiles) or vertical velocity metrics (if working with low-resolution dive profiles). Moreover, this method represents a powerful tool for detecting foraging activity of marine species with a more classical diving behaviour (*e.g.* SES; tend to forage in the bottom phase of dive), but also for species with greater dive behaviour complexity (*e.g.* Weddell seal; foraging occurs in several parts of the dive). Finally the "hunting time" is a simple metric that is easy to integrate into ecological studies (*e.g.* Paper 5) and/or that can be used in combination with other diving metric depending on the study objectives (*e.g.* Viviant *et al.* 2014 for predictive models of foraging success) .

1.1.2 Disadvantages of the hunting method

"Hunting" parts of high and low-resolution dives were associated with most prey capture attempts (estimated independently from acceleration data). The detection of "hunting" segments therefore provides information on parts of the dive where prey encounters are likely to occur. However, the "hunting time" cannot be used as an index of foraging success as it does not predict the number of prey captures attempted during a dive. Indeed, some "hunting" segments can be long but only associated with a few prey capture attempts (PrCA), whereas some "hunting segments" can be short but still be associated with numerous PrCA. Obviously, the contrary is also true. This is likely to depend on physiological constraints and the quality of the patch encountered, which is already known to influence dive duration and bottom time (see Dragon *et al.* 2012a; Thums *et al.* 2013; Viviant *et al.* 2014). Thus, "hunting time" should be used as an index of dive foraging effort which includes the time spent pursuing, and potentially encountering, a prey, but not an index of the number of PrCAs per dive and/or foraging success.

1.2 Detection and prediction of foraging success

Recently, Viviant *et al.* (2014) developed predictive models to estimate the number of PrCA (estimated from acceleration data) using diving metrics at different scales (*e.g.* dive, bout, several time intervals and night). This method reveals promising results as it would allow the estimation of foraging success from time-depth data only. Such data are already widely available for many species, over extensive areas and multiple years and would contribute significantly to future large scale studies. However, the authors highlighted the necessity to validate these models at a species level to find the appropriate diving metrics for a given species. Moreover, they stated a poor predictive power at the

dive scale, which could be, to our point of view, discouraging considering the number of metrics included in the model (*i.e.* descent and ascent rates, number of steps at the bottom of the dive, surface duration, maximum dive depth, dive duration, depth variations at the bottom of the dive and bottom duration). The inclusion of the "hunting time" foraging effort metric could mean a reduction in the number of metrics included in the model and could simplify its application. However, before using a similar approach on the Weddell seals, the acquisition of acceleration datasets for several individuals is needed for further validation. Moreover, because of the small scales of their foraging range we would need to obtain good predictive models at the dive level. Other proxies of foraging success (*e.g.* increase in body condition, gain in lipid stores), that can be calculated using time-depth data, have been developed for SES and northern elephant seals (*Mirounga angustirostris*) (Biuw *et al.* 2007; Robinson *et al.* 2010; Thums *et al.* 2011; Schick *et al.* 2013). These proxies rely on the detection of changes in body condition as inferred from drift-dive behaviour. Unfortunately, this type of behaviour is not exhibited by the Weddell seals and thus cannot be applied to this species.

Without direct or indirect measurements of prey encounters from equipment such as video cameras, jaw movement sensors, stomach thermometers or head accelerometers it is difficult to assess Weddell seals' foraging success (Davis *et al.* 1999; Horsburgh *et al.* 2008; Naito *et al.* 2010; Gallon *et al.* 2012). Although these methods are attractive, there are two main limitations of these techniques to conduct ecological studies such as presented in Paper 4 and 5. First, these loggers often only record and store data over short periods of time and cannot detect foraging activity during the whole winter season for large number of individuals (until really recently; see Watanabe & Takahashi 2013). Second, when studying the behaviour of species that evolve in sea-ice covered areas and do not necessarily return to an accessible colony (*i.e.* Weddell, Ross, crabeater and leopard seals),

the probability of logger retrieval (needed to access the data) is quite low. A new generation of tags that allow the recording and direct satellite transmission of acceleration data associated with the dive profiles could overcome these constraints (C. Guinet pers. com.).

Considering the current logger technology and analysis methods available to detect foraging activity, the foraging effort metrics developed and selected in this study were a good compromise given the dataset constraints and ecological questions we had. However, it provides exciting perspectives for future studies on the foraging behaviour of Weddell seals, which is discussed later in this thesis.

2. Track analysis and implementation of the foraging effort index

The second main constraint of our dataset resided in the quality of the locations provided by the Argos system that can be associated with high or non-estimated measurements errors. Indeed, in habitat use/selection studies, extracting environmental information at highly uncertain Argos locations increases the probability of extracting the wrong information. This spatial uncertainty poses a serious challenge as it can lead to inaccurate assessments of environmental influences on animal behavioural responses. This can become increasingly problematic for species like the Weddell seal which move within a comparatively small spatial range, in contrast to the southern elephant seal for example, which travels thousands of kilometres from their colony site. Other inherent characteristics in Weddell seal behaviour needed to be taken into account in our assessment of their response to the environment. For instance, Andrews-Goff *et al.* (2010) showed that haul-out locations were over represented in the dataset. The inclusion of these locations in the

analyses could lead to a bias towards the importance of haul-out behaviour rather than their diving and foraging behaviour. Moreover, Weddell seals move in sea-ice covered water which can constrain their movements as they rely on breathing holes to breathe. This is in contrast to species that forage in open waters and are unimpeded by such barriers. This important difference needs to be taken into consideration when defining ARS and relating them to particular environmental features. To address these issues we adapted our analyses, in several ways, to limit the inclusion of behavioural and environmental bias.

Firstly, state-space modelling approaches (*i.e.* Kalman filter and correlated random walk models) were applied to the Weddell seal tracks in order to minimize the error associated with Argos locations (Johnson *et al.* 2008; Patterson *et al.* 2010). The resulting locations from these models have proven to be a vast improvement on Argos locations when compared to GPS tracks (Andrews-Goff 2010 [PhD]; Patterson *et al.* 2010). Studying the haul-out behaviour of Weddell seals during winter was not the purpose of this study and has already been investigated using telemetric data at the Davis site (Lake *et al.* 1997, 2005; Andrews-Goff *et al.* 2010). Therefore, to avoid haul-out behaviour bias we excluded haul-out periods from our dataset.

Secondly, two approaches were used to take into account the remaining error associated with each location when extracting environmental variables. In the first approach the extracted environmental variable was weighted by each location's error distribution (Paper 4 and see Andrews-Goff 2010 [PhD]). In the second approach, the fitted correlated random walk model was used to simulate each track 100 times. Environmental variables were then extracted for each simulation of each location and averaged at each dive main location (Paper 5, Johnson *et al.* 2008). In both cases, the environmental variables were averaged from all the values included in the Kalman error ellipse associated with each filtered location. Despite these procedures, combined errors from both seals'

locations and mainly environmental variable resolutions remained (*e.g.* resolution of the bathymetry). For instance, we had to remove 25 % of the dives because diving depths were abnormally deeper than the bathymetry or dives were located on land. This demonstrates the advantage of deploying fast-loc GPS combined with Argos tags to conduct habitat use studies. It is especially true for species with small scale displacements such as the Weddell seals when accuracy becomes increasingly important when extracting environmental variables.

The SSMs have proven to be efficient in detecting foraging activity in several species such as the SES which exhibit long range displacement (Jonsen *et al.* 2005, 2007; Dragon *et al.* 2012b). However, when applied to Weddell seals, SSMs indicated that the seals were almost continuously in a state of "search" (Andrews-Goff 2010 [PhD] and S. Bestley *unpublished data*). This is likely a bias due to the very small distances the Weddell seals from DDU and Davis travelled daily (DDU: ~ 4 km/day and Davis: ~ 11 km/day) and a high sinuosity of their trajectories. This suggests these SSMs are not appropriate for local foragers. As an alternative, we opted for a FPT-derived analysis in which we included the "hunting time" (*i.e.* called first hunting time analysis or FHT; see Paper 5). The integration of a vertical foraging metric allowed for the assessment of ARS behaviour according to the foraging activity occurring at depth (where prey captures occur). It also limited ARS bias induced by the presence of sea-ice which can constrain seals' movements and lead to the detection of false ARS (see Paper 5 and Bailleul *et al.* 2008). Although the FHT analysis presented some advantages (*i.e.* optimal ARS scale, simplicity of the method, straightforward results) it is challenging to include the FHT values in a powerful habitat use model without risking to violate some statistical rules (see Freitas *et al.* 2008; Zuur *et al.* 2009, 2010). The inclusion of FHT values in mixed models was made possible by transforming the FHT values into a binomial variable. However, generalized mixed effect

models for binomial family are still under development and only one type of model ("glmPQL") included an auto-correlation term (which is vital for time series datasets such as those in this thesis). Although the "glmPQL" (R library "MASS") provides similar results to the "lmer" (R library "lme4") (see Zuur *et al.* 2009), this model did not calculate either a AIC or BIC which would have helped in the model selection process. Consequently, further studies should investigate how to integrate the "hunting time" vertical foraging effort metric (and other diving metrics) and environmental parameters in a Bayesian state-space modelling approach as done by Bestley *et al.* (2012) for the SES. This would allow researchers to assess, with a single model, which diving and environmental variables induce a switch toward intensive foraging (Bestley *et al.* 2012).

B - Ecology of the Weddell seal during winter

1. Context

Organisms that optimize resource acquisition in the environment are expected to increase their chances of reproductive success and survival, thereby increasing their fitness (Stearns 1992). Thus, in an environment where resources are limited, each species actively select the series of biotic and abiotic conditions (*i.e.* habitat) associated with the resources needed to meet its requirement (Krausman 1999). Habitat selection is therefore an active behavioural process that results from innate and learned behaviours (Wecker 1964). These behaviours can be reflected by the spatial and temporal distribution of foraging effort, the type and quantity of prey captures as well as predation and competition avoidance.

The life of the Weddell seal during spring and summer, when they breed and moult in human accessible parts of the fast-ice, is well known (Kooyman 1981). However, most of the energy stores for these activities are gained during February to October when they spend most of their life cycle at sea and few studies can be made (Kooyman 1981; Castellini *et al.* 1992a; Testa 1994b). Studying Weddell seals' behaviour and ecology during the winter period is crucial to better understanding their role in the Southern Ocean ecosystem and to understanding how biological and physical elements of that ecosystem ultimately influence the behaviour and population characteristics observed in spring and summer (Testa 1994b). **The aim of this PhD was therefore to improve our understanding of Weddell seals' winter ecology and how they optimize their foraging strategies during winter. This is what we will try to assess in this discussion.**

2. The fast-ice: a primary habitat for Weddell seals

2.1 Movement patterns of Weddell seals during winter

In contrast to other species that forage both during winter and the breeding seasons (*e.g.* Adélie and emperor penguins), female Weddell seals (the focal animal studied in this thesis) will fast during most of the pup-rearing period (Testa *et al.* 1989; Costa 1991; Wheatley *et al.* 2008). Thus, they need to maximize their foraging success during winter in order to ensure their breeding success. On the other hand, not having to constantly return to a specific colony while foraging allows Weddell seals to have a greater freedom in their displacements in contrast to the emperor penguins, which are tightly linked to their colony due to egg- (beginning of winter) or chick-rearing (end of winter) (Burns & Kooyman 2001). To date, only a few studies have followed the movement patterns of Weddell seals during winter. In the Ross Sea, satellite telemetry studies showed that although Weddell seals remained close to their summer breeding site, both adults and juveniles also travelled long distances to use the deep pack-ice as well as polynyas in the case of juveniles (Testa 1994b; Burns *et al.* 1999; Stewart *et al.* 2000). In the Vestfold Hills near Davis station, previous studies showed that Weddell seals were mainly hauling-out and using the fast-ice area (Lake *et al.* 2005, 2006). However, long gaps in the locations dataset induced Lake *et al.* (2006) to state that Weddell seals would travel to the pack-ice to forage but return to the fast-ice to rest. Our studies revealed that both seals from DDU and Davis remained in the coastal fast-ice area even if the animals from Davis travelled longer distances (see Paper 4 and 5). **The ice cover represents a barrier between two essential components of their environment: the air where they breathe and the water column where they feed. Thus, the fact that the primary habitat of overwintering Weddell seals is the coastal fast-ice raises some questions: Why would an air-breathing species remain in an area where**

finding access to breathing holes becomes limited as the sea-ice thickens during winter? How do they use this fast-ice habitat to find areas where they will be both able to breathe and find food?

2.2 Overwintering in fast-ice allows predator and inter-specific competition avoidance

The local and coastal winter habitat use of Weddell seals is quite different to the winter behaviour of the other sea-ice obligate seal species (Tynan *et al.* 2009). Indeed, the crabeater, leopard and Ross seals overwinter in the pack-ice area where the sea-ice is thinner. The majority of crabeater seals stayed within 300 km of their tagging location (Burns *et al.* 2004) and leopard seals tend to disperse northwards during winter, most likely in relation to the winter ice edge (Jessopp *et al.* 2004). Similar to the leopard seal, Ross seals migrate north in winter, likely to access the area between the northern limit of the pack ice and the Antarctic convergence (Jessopp *et al.* 2004). In addition, Adélie penguins and minke whales also overwinter in the pack-ice (Tynan *et al.* 2009). The key difference between the Weddell seals and other Antarctic sea-ice obligate predator species (*e.g.* penguins and seals) is their ability to maintain breathing holes in the ice by abrading the sea-ice with their teeth which allows them to inhabit the fast-ice environment year-round (Kooyman 1981). The emperor penguin is the only other species foraging in the fast-ice area during winter. However, despite similarities in their diving behaviour and diet, Burns & Kooyman (2001) found little trophic overlap between the two species due to geographical and seasonal differences in habitat use. For instance, while female emperor penguins travel to the pack-ice to forage, Weddell seals remain close to the coast (Burns & Kooyman 2001). **Thus, their occupation of the winter fast-ice environment reduces**

inter-specific competition and provides additionally shelter from killer whale predation. Because predation and resource competition with other species is probably minimal we expect environmental conditions to be a major driver of habitat selection and how they use these areas

2.3 Assessment of important sea-ice features to Weddell seals

In the fast-ice environment, where open water can be a limiting resource for air-breathing predators, polynyas offer ideal access to open water and could facilitate accessibility to the under-ice ecosystem (Tynan *et al.* 2009; Massom & Stammerjohn 2010). Davis and DDU are both known to be associated with recurring polynyas (Arrigo & Van Dijken 2003), and a study in George V Land (close to DDU) showed large concentrations of Adélie and emperor penguins, crabeater seals and also few minke whales in the vicinity of the Mertz Glacier polynya (McMahon *et al.* 2002). We therefore expected Weddell seals from both focal sites to favour or remain close to open water areas, similar to the juveniles in McMurdo (Stewart *et al.* 2000). While a small coastal polynya at the Davis site seemed to attract several actively foraging individuals, most hunting dives (as well as transit dives) were still associated with highly concentrated sea-ice at both sites (see Paper 5). Therefore, it appears that the presence of polynyas is not the major sea-ice feature driving Weddell seal habitat selection.

Surprisingly, sea-ice concentration did not influence either Weddell seal diving or foraging behaviour (Paper 4 and 5). However, our study along with studies conducted in McMurdo (Testa 1994b; Burns *et al.* 1999; Stewart *et al.* 2000), show that Weddell seals

exploit their sea-ice environment differently according to the location and its distinct sea-ice conditions. For instance, sea-ice conditions at the DDU site was less variable both spatially and temporally, and the seals travelled less and they mainly foraged in restrained areas compared with the Davis site. This suggested that although sea-ice concentration did not influence Weddell seal's behaviour, some sea-ice features such as open water areas and/or sea-ice variability could influence Weddell seal's movement patterns and habitat use. Including these sea-ice derived parameters in our analyses showed Weddell seals from DDU tended to forage more when closer to open water areas, whereas Weddell seals from Davis tended to forage more in less variable sea-ice in space (within 25 km). These results, which considered the 3D Weddell seals' behaviour are concordant with two hypothesis on Weddell seals' sea-ice utilization. **First, Weddell seals are more likely to be influenced by sea-ice thickness (rather than just sea-ice concentration itself) which needs to be thick enough to ensure a stable haul-out platform, but thin enough to allow them to maintain their breathing hole without it being detrimental to their survival by damaging their teeth** (Stirling 1969; Lake *et al.* 2005, 2006)**. Second, the seals are probably responding to smaller features within the fast-ice environment such as the presence of perennial tide cracks which would not be depicted by the coarse resolution of the sea-ice data available to us.**

The importance of these cracks to Weddell seal ecology has been illustrated recently in McMurdo Sound (Siniff *et al.* 2008; Chambert *et al.* 2012). In 2000, the large iceberg B-15 became grounded across the entrance of the McMurdo Sound and induced changes in sea-ice conditions, resulting in thicker ice and narrower tide cracks, preventing the seals from maintaining their breathing holes (Siniff *et al.* 2008). Consequently, during most iceberg years, Weddell seals were less abundant in the area and exhibited low reproductive success (Chambert *et al.* 2012). Weddell seals are likely to remember the locality of tide

cracks from previous experience and therefore rely on them from one year to another to breathe and forage (Kooyman 1981; Tynan *et al.* 2009). This is supported by the pluri-annual site fidelity observed in our studies and their close proximity to land. This pattern was even more pronounced in DDU where sea-ice conditions are less variable both in space and time, resulting in fewer suitable sites for both breathing and foraging compared to in Davis. The presence of land is likely to be associated with thinner sea-ice because tidal action constantly push the annual ice away from shore or around small offshore islands, which could be used by the seals as a cue for suitable ice-conditions (Lake *et al.* 2005; Tynan *et al.* 2009). Indeed, experiments conducted on Weddell seals from an isolated hole found that if the seal was able to see land from the hole it would leave and be later found around tide cracks closer to the coast (Kooyman 1981). These experiments also suggest that Weddell seals use landscape features to orientate themselves visually. **The fact that seals return to the same areas on a pluri-annual basis and their proximity to land (Paper 4 and 5) suggest that the preferred habitat of Weddell seals within the fast-ice is where environmental forces crack the fast-ice, thereby allowing them access to profitable habitat.**

3. Foraging strategies of Weddell seals

Bailleul *et al.* (2008) suggested that in highly concentrated sea-ice, air-breathing mammals such as the SES could become "central place breathers" that are dependent on their ice-hole or cracks regardless of the foraging quality of the area. However, our results suggest Weddell seals would not return to an area from one year to the next if it was not considered productive by the individual. This is also true for Weddell seals that are

observed from year to year in McMurdo Sound (Kooyman 1981). Moreover, the neritic ice-covered area represents a reliable source of food during winter for species that have the capacity to utilise this environment, such as the Weddell seal (see Part I section "sea-ice dependant ecosystem") (Smith *et al.* 2007; Tynan *et al.* 2009). It is more likely that Weddell seals have evolved or learned behavioural tactics (that will be discussed below) in order to maximize food acquisition within the range of constraints imposed by the environment and their physiological abilities (*e.g.* finding a breathing hole, minimizing travel costs, targeting prey within their depth range).

3.1 Optimal foraging from a breathing hole

Kooyman (1975) proposed that Weddell seals foraging beneath fast-ice will dive from a breathing hole until resources within its accessible radius become depleted. In our study, the errors associated with Argos locations did not allow the distinction between individual breath-access holes because we were unable to determine if two locations separated from less than 2 km were actually corresponding to different breathing holes. We were therefore not able to discriminate dives according to the hole they were performed from. To do this accurately, a GPS dataset of locations would be needed. Instead, we used the FHT analysis which enabled us to identify the optimal scale at which seals concentrated their dive search effort. At both study sites, the optimal ARS scale (~4-5 km) corresponded to the range of distances that a seal could travel underwater between breathing holes in a single breathe (Kooyman 1981; Davis *et al.* 2003). Rather than returning exactly to the same breathing hole as seals diving from an isolated hole would do (Kooyman 1968, 1975) it is likely that free ranging seals travel between a network of holes close to each other. Although the ARS optimal scales were similar at Davis and DDU, seals from Davis spent

less time foraging in an area of a given radius (~4 hours in Davis versus ~11 hours at DDU). This could be due to faster prey depletion (because there are less prey or prey are more accessible and captured fatser) in a given area in Davis or it could be related to different environmental conditions that could influence prey availability and/or accessibility. Based on our evidence the latter is perhaps more plausible as we showed contrasting sea-ice conditions between DDU and Davis, in which Davis sea-ice conditions were more variable (see paper 5).

Travelling between holes represents a risk of disorientation and/or reaching an area covered of thick ice that would be costly to open and maintain. The marginal value theorem is one of the most familiar models used to predict how long a forager should stay in a patch (Charnov 1976). To maximize resource intake within a patch, a predator's residence time should be related to the cost of travel to the patch. Therefore, if the quality of a patch decreases (*e.g.* drop in abundance and/or prey type switch) a predator should then leave (Charnov 1976). For Weddell seals, the risk taken to travel to another breathing hole could be considered as an additional cost to the total (horizontal + vertical) travel cost to reach a patch of prey. Therefore, in an environment where travelling costs between prey patches could be high (*e.g.* DDU where sea-ice is less variable), we expect a predator to increase its time spent searching for prey even if the patch quality decreases (*i.e.* seals in DDU spent twice much time hunting in a given area then in Davis where the sea-ice is more variable).

3.2 Inference on Weddell seals' diet from diving behaviour

The preferred foraging depth of a deep diving predator is generally influenced by both predator diving capacity and prey distribution (Burns & Kooyman 2001; Watanabe *et al.* 2003). Studies on the diet of Weddell seals suggest individuals switch foraging techniques

according to prey availability as well as possible competition between individuals. For instance, Plötz *et al.* (1991) showed Weddell seals from the Weddell Sea would switch from pelagic foraging on *P. antarcticum* one year to targeting almost entirely benthic fish the next. Moreover, Weddell seals from McMurdo Sound have been shown to feed predominantly on *P. antarcticum* in summer (Diet analysis, Burns *et al.* 1998). Testa (1994) inferred from their diving behaviour that *P. antarcticum* should also be an important winter prey, as well as other mid water species such as squid. However, their diving depths indicated that they may occasionally switch to feeding on benthic prey (Testa 1994b).

The focal Weddell seals in this thesis used both pelagic and benthic strategies, reflecting the opportunistic nature of their feeding (Paper 4 and 5). The complexity of their diving behaviour (Paper 2 and 3) also supports these findings. Because we lack detailed diet analysis concurrent with their at-sea foraging behaviour we are unable to draw firm conclusions on the type of prey targeted by the focal Weddell seals. However, considering their dive behaviour (i.e. complexity, depths targeted), as well as some preliminary diet analyses (V. Andrews-Goff and Y. cherel, *unpublished data*), allow us to make some inferences on the prey type targeted. Stable isotopes analyses on the seals from DDU are concordant with a pelagic diet of high trophic level prey such as *P. antarcticum*, *Dissostichus mawsoni* and cephalopods (Y. cherel *unpublished data*). Preliminary scat analyses suggested that benthic prey could include *Trematomus* spp, and *Channichthyidae* spp. (V. Andrews-Goff *unpublished data*). Moreover, most seals essentially performed pelagic dives (28 seals out of 32) and the depths targeted (~115 m (DDU), 179 m (Davis)) are concordant with foraging on mid-water prey, even if high variability between individuals existed. These depths are similar to the depths reached by the seals from McMurdo during winter (Castellini *et al.* 1992a; Testa 1994b), as well as the depths reached by emperor penguins that are also known to forage on *P. antarcticum* (Cherel & Kooyman

1998). In addition, Weddell seals from DDU dived deeper and longer during the day than at night and in both location pelagic dives occurred essentially at night. Diurnal dive patterns have been observed in SES, Antarctic fur seals and crabeater seals that all forage on prey exhibiting nycthemeral migrations with prey being closer to the surface at night and deeper in the water column during the day (*e.g.* Antarctic krill and myctophid fish in the case of SES) (Boyd & Croxall 1992; Lea *et al.* 2002; Burns *et al.* 2008; Biuw *et al.* 2010). In our study the diurnal patterns exhibited by Weddell seals are consistent with seals foraging mainly on prey that display vertical migration in direct relation to light intensity, such as *P. antarcticum* (Fuiman *et al.* 2002). At Davis, while pelagic dives mainly occurred at night (suggesting a consumption of *P. antarcticum*), benthic dives occurred equally during the day and at night which suggests seals at Davis have a more varied diet than the seals at DDU. This is likely due to the larger range of areas explored by the seals from Davis. For instance, previous studies reported Davis Weddell seals foraging in the southern fjords and inshore areas mostly consumed benthic fishes and prawns, whereas in the northern and offshore areas their diet was dominated by *Pleurogramma antarcticum* (Lake et al. 2003, Green and Burton 1987).

Our findings suggest that Weddell seals from both locations forage on mid-water fish which is consistent on the Antarctic shelf, with a diet dominated by *P. antarcticum* (see Part I, section "sea-ice dependant ecosystem"). **However, the variability of foraging patterns both within and between individuals showed Weddell seals are also opportunistic feeders throughout winter. This could be a strategy for adjusting foraging behaviour in response to strong intra-specific competition and/or inherent constraints in an ice-covered environment.** It is likely that intra-specific competition is an important driver of foraging behaviour as Weddell seals remain close to their tagging locations and presumably concentrate around a limited number of breathing holes and

cracks to access air between dives (Kooyman 1981; Hindell *et al.* 2002). Moreover, if a target prey species is depleted in the vicinity of a breathing hole (*e.g.* intra-specific competition, intensive use of this area by an individual or several), but the seal is unable to move to another hole due to heavy sea-ice conditions, then we suggest that the seal can switch to another target prey species. Indeed our analysis of their foraging behaviour provides evidence to support this notion. However, it highlights the need for detailed diet analysis to be conducted concurrently with seal foraging behaviour to fully understand the range of foraging behaviours exhibited.

3.3. Weddell seals' adaptation to winter conditions

Emperor penguins and Weddell seals are the only air-breathing, warm-blooded predators remaining in the fast-ice area during winter (Burns & Kooyman 2001). The fact that emperor penguins brood their egg and chick throughout Antarctic winter is the best illustration of their adaptation to this extreme environment. Weddell seals, on the other hand, take advantage of low inter-specific competition by remaining in the fast-ice environment when all other marine mammals have left the region. Although this results in exposure to harsh environmental conditions associated with the continental Antarctic winter, the physiological adaptations of the Weddell seal allows them to resist the cold and hunt underneath the sea-ice (Kooyman 1981). Moreover, our work suggests that Weddell seals evolved and/or learned behavioural responses that allow them to store the energy needed for the breeding season. So far we have suggested that Weddell seals favour fast-ice areas likely associated with predictable cracks, tend to modify their search effort according to sea-ice conditions, as well as modify their foraging behaviour to prey. We will now discuss how they respond to the advance of winter.

We showed that Weddell seals from both Davis and DDU were more likely to display ARS behaviour with the advance of winter (Paper 5). In addition, we showed that seals dive shallower and for longer without increasing dive foraging effort as winter advances (Paper 4 and 5). This means that Weddell seals are likely to spend more time hunting in a given area with the advance of winter. In addition, Andrews-Goff *et al.* (2010) found that Weddell seals were less likely to haul-out as air temperature dropped and wind speed increased during winter. They also showed Weddell seals switched from diurnal haul-out behaviour during summer to a hauling-out nocturnally during winter (Andrews-Goff *et al.* 2010).

From these observations we suggest the increasing probability of being in ARS with the advance of winter is the results of a combination of parameters. Firstly, Weddell seals spend more time underwater to avoid harsh weather conditions, and while diving, also search for prey. The advance of winter also coincides with the approaching calving season and female Weddell seals are likely to increase their search effort in order to store energy before giving birth, followed by the pup-rearing period in which they mostly fast. Moreover, by increasing their search effort Weddell seals can compensate for possible prey depletion as prey acquisition is likely to increase with search time (Kramer 1988; Houston & Carbone 1992). Lastly, they are likely to maximize their time searching for prey in a given area because the risk of leaving a breathing hole for another area becomes higher as the sea-ice becomes thicker throughout winter (as discussed in section "optimal foraging from a breathing hole"). The latter is likely to also be related to the switch observed in diving behaviour (*i.e.* increase in dive duration but decrease of depth to maximise the horizontal distance covered). Indeed, Weddell seals are more likely to increase the time spent travelling and orientating themselves at each breathing hole as sea-ice thickens and light intensity decreases and with winter. Wartzok *et al.* (1992) found that Weddell seals

and their Arctic counterpart, the ringed seals (*Phoca hispida*), were essentially using visual cues to orientate themselves under the sea-ice to find their holes again after a dive. They also showed that when surface visibility was several hundred meters or more Weddell seals returned to their hole at angles up to 75° from departure. In contrast, when the visibility was lower than 100 meters (which is likely to be the case in winter) the leave-return angles were no more than 15° (Wartzok *et al.* 1992). This type of behaviour would increase the duration of the dive, but the oxygen store used to travel almost parallel under the ice cannot be used to reach great depths, resulting in shallower dives during winter. On the other hand, by essentially diving during light hours (and hauling-out during the night) Weddell seals optimize their foraging strategy as they can use improved visibility conditions to locate and pursue their prey, as well as orientate themselves better under the ice. **Despite harsh winter conditions, these different tactics show how Weddell seals are likely to adapt to the winter environment to optimize the trade-off between locating breathing holes and maximising prey acquisition.**

3.4 Environmental parameters influencing the behaviour of Weddell seals

In open water environments, the behaviour of top predators can be influenced by several oceanographic features such as fronts, eddies, sea surface height, water column temperatures and chlorophyll concentrations (Guinet *et al.* 2001, 2014; Bost *et al.* 2009; Bailleul *et al.* 2010b; Dragon *et al.* 2010; Biuw *et al.* 2010). However, within the sea-ice region, especially during winter, these environmental features become less relevant for two reasons: (1) most of these features cannot exist due to extensive sea-ice cover, and (2) extended periods of darkness during the polar winter is associated with reduced

productivity. In addition, data on biotic parameters such as chlorophyll become increasingly scarce as heavy sea-ice limits ship surveys and satellite coverage, particularly during winter months. However, we know that in winter the water temperature profile becomes homogeneous in areas explored by the seals (*unpublished data*), and that oceanographic features are instead largely driven by changes in salinity during sea-ice formation, which in turn allows the formation of distinct water masses (see Part I).

We showed for the first time that Weddell seal diving behaviour was influenced by such water masses and that they tended to favour warmer and less dense water according to their seasonal succession. During winter they mainly used the MCDW, which is likely to upwell in response to the bathymetric features associated with the main areas targeted by the seals (see Paper 4). The importance of this water mass to the Antarctic ecosystem have been highlighted in previous studies (Tynan 1998; Prézelin *et al.* 2000; Ducklow *et al.* 2007) and is known to be associated with the foraging behaviour of other top predators such as SESs while foraging on the shelf break (Muelbert *et al.* 2013, Labrousse et al. *submitted*). This nutrient-enriched water mass could stimulate productivity (Sievers & Nowlin 1984; Prézelin *et al.* 2000), thereby attracting zooplankton and fish therefore providing a predictable source of food for top predators. It is not known if this holds true for winter because of limited light availability, however, juvenile *P. antarcticum* have been found in association with this water mass on the continental shelf (La Mesa *et al.* 2010). Interactions between bathymetry and water mass boundaries may also aggregate prey which could result in specific assemblages of species attracting Weddell seals (Burns *et al.* 2004; Zhou & Dorland 2004; Ribic *et al.* 2008). Finally, the warmer MCDW could interact with sea-ice and facilitate the formation of cracks in the ice which would be particularly important for Weddell seals (Lake *et al.* 2005, 2006; Nicol *et al.* 2006; Tynan *et al.* 2009).

The importance of bathymetric features to top predators has already been highlighted (Burns *et al.* 2004; Chapman *et al.* 2004; Ribic *et al.* 2008; O'Toole *et al.* 2014). Andrews-Goff (2010, PhD) showed that foraging Weddell seals predominately occupied shallow areas (as estimated from kernel density plots) but could not conclude why these areas may be important in relation to their foraging activity. In this thesis, the use of metrics such as vertical ARS and time spent at depth allowed us to identify important foraging grounds on the basis of their foraging behaviour, rather than solely based on their horizontal displacement (i.e. density of their distribution). We therefore demonstrated that shallow areas represent favourable foraging grounds for the Weddell seals, a pattern that has been observed for other species of seals and seabirds (Burns *et al.* 2004; Muelbert *et al.* 2013; Raymond *et al.* 2014). Indeed, the bathymetry could induce upwelling of the MCDW mainly used by the Weddell seals from DDU (we do not have similar data for the Davis site), facilitate prey accessibility and capture, as well as allowing seals to switch from one foraging strategy (*i.e.* switch from pelagic to benthic foraging) to another according to prey availability in the water column. Kooyman (1981) also suggested Weddell seals used bathymetric features, which they probably memorize from the first dives they make from a breathing hole, to orientate under the sea-ice gallery. We therefore speculate that foraging over shallow areas would also allow Weddell seals to optimise movement in the underwater environment and reduce foraging costs compared to those in deeper areas (although deep areas were available they were not used by the focal seals for foraging).

Weddell seals seem to use environmental features as cues to find favourable areas where prey accessibility and availability would be facilitated and/or induced. In addition, environmental features that interact with sea-ice conditions and facilitate under-ice orientation could also help Weddell seals to find suitable patches that provide adequate breathing holes and prey resources.

C – Conclusion and Perspectives

1. Main conclusions

The methods developed and used in this thesis allowed identification and quantification of the winter foraging activity of Weddell seals according to their environment. Our study demonstrated some of the key foraging strategies showing Weddell seals' adaptation to the Antarctic environment, not only because of evolved physiological traits (*i.e.* ability to thermo-regulate in extreme cold and dive underneath the ice), but also because they actively optimize their spatial use of the fast-ice environment in both the temporal, horizontal and vertical dimensions. Our results also suggest Weddell seals adapt their foraging behaviour in response to physical parameters of their environment that are likely to be associated with better prey availability and accessibility, as well as regular access to breathing sites. These physical conditions are influenced by features in the fast-ice, topography and hydrology. At finer scale the foraging behaviour of Weddell seals appear to respond to the distribution and availability of prey in the water column (*i.e.* switching from pelagic to benthic foraging, exhibiting diurnal behaviour, and the complexity of the dives). The fact that juveniles are rarely observed in the fast-ice environment during winter (Kooyman 1981; Stewart *et al.* 2000) suggest these tactics have been learned from previous experience. Therefore, it would be necessary to equip individuals from different age classes to compare the strategies adopted by each cohort.

Our results also showed the ability of the Weddell seals to adopt different foraging strategies within and in between sites (*e.g.* display a range of movement patterns, variable diving depths and durations, as well as pelagic and benthic diving behaviour). This indicates some level of phenotypic plasticity within and between the populations at DDU

and Davis. Such plasticity allows a population to shift in response to different environmental conditions through modifications to phenotypic traits (*e.g.* anatomical, morphological, behavioural and physiological) (Bradshaw 1965; Terraube *et al.* 2011; Chambert *et al.* 2012). This has important implications for the conservation and predictions of potential climate change effects on this species. Indeed, it is possible that Weddell seal populations at different locations (*e.g.* Antarctic Peninsula, Weddell sea, McMurdo Sound, DDU and Davis) and individuals within each population may respond differently to changes in their environment.

2. Climate change and Weddell seals

2.1 Observed changes in Antarctic sea-ice

Changes in Antarctic sea-ice extent and seasonality have been monitored during the last few decades, and contrasting trends have been observed depending on the Antarctic regions considered. While sea-ice extent and persistence has been increasing in the Ross Sea and the Weddell Sea, the reverse trend has been observed in the Antarctic Peninsula sectors (Stammerjohn *et al.* 2012). Studies have shown that these changes have already negatively impacted some top predator species. For instance, in the Western Antarctic peninsula the decrease in sea-ice extent and duration has resulted in the current decline of krill-dependant species such as Adélie and Chinstrap (*Pygoscelis antarctica*) penguins, and Antarctic fur seals (from South Georgia) presumably due to a decrease in krill (Forcada *et al.* 2005; Trathan *et al.* 2007; Trivelpiece *et al.* 2011; Lynch *et al.* 2012). In the Ross Sea, the northward extent of sea-ice has been shown to be detrimental to Adélie penguins by preventing juveniles to access the deep pack-ice before winter where they will forage on

abundant Antarctic krill (Wilson *et al.* 2001; Lyver *et al.* 2014). In East Antarctica, there is no clear sea-ice effect on krill biomass or top predators (*i.e.* indirectly relying on krill biomass via the trophic web) despite a small increase in sea-ice extent over the last three decades (Turner *et al.* 2009; Nicol & Raymond 2012; Massom *et al.* 2013).

2.2 Assessment of potential climate change effects on Weddell seals

The Weddell seal, like other sea-ice obligate seals, relies on sea-ice for all its life history traits. Therefore, changes in sea-ice conditions such as its extent, seasonal persistence and thickness could impact the population dynamics of Weddell seals (Siniff *et al.* 2008). For instance, less Weddell seals have been observed in the Antarctic Peninsula, likely due to the reduction of fast-ice needed for breeding (Siniff *et al.* 2008). In McMurdo Sound, long-term monitoring of the Weddell seal population revealed the effect of sea-ice-related factors on population dynamics (Cameron & Siniff 2004). Indeed, Testa *et al.* (1991) linked the El Niño Southern Oscillation (ENSO) to Weddell seal population dynamics. It is thought that the impact of this broad-scale climatological event is mediated trough changes in sea-ice extent and concentration (Siniff *et al.* 2008). A similar trend has been postulated for the Weddell seals in the Vestfold Hills (Lake *et al.* 2008). At McMurdo, L Hadley *et al.* 2007 and Proffitt *et al.* (2007) also demonstrated that extensive sea-ice during the post-weaning period negatively impacted the reproductive success of pregnant females. In contrast, years of extensive winter sea-ice were followed by years of higher survival rates among adult females (Hadley *et al.* 2006). In McMurdo Sound the calving of icebergs from the Ross Ice Shelf resulted in increased ice thickness of near-shore ice and the disappearance of predictable tide cracks in the ice used to access preferred pupping sites (Siniff *et al.* 2008).

Consequently, during the years the B-15 iceberg was grounded in the sound (from 2000 to 2006), female reproductive rates dropped but adult survival appeared unaffected (Chambert *et al.* 2012). Despite dramatic effects of the B-15 iceberg on the nearby emperor penguin population (*i.e.* adult breeding failure and high chick mortality; (Kooyman *et al.* 2007)), Chambert *et al.* (2012) demonstrated Weddell seals managed to avoid survival costs and rapidly re-achieved high levels of reproduction by the end of the perturbation.

As for most Antarctic species, it is difficult to estimate the Weddell seal population trend because of several factors including: the immensity of the Antarctic continent; access difficulties; and the proportion of diving animals compared to the animals hauling-out (Southwell *et al.* 2012). However, long-term monitoring of the Weddell seal population in McMurdo Sound and DDU showed that the populations were overall stable (Rotella *et al.* 2009), UMS pelagis *unpublished data*). **The unique acclimation abilities of Weddell seals observed in McMurdo as well as the behavioural plasticity demonstrated in this thesis suggest that Weddell seals are likely to be more robust against climatic changes as they can occupy a range of habitats and can target a larger range of prey types than specialist feeders (*i.e.* Adélie penguins, crabeater seals) (Laidre et al. 2008). However, long-term climate change that increases near-shore ice thickness and/or modifies the prevalence or persistence of fast-ice could negatively affect Weddell seals.**

3. Perspectives

3.1 Information on prey: the missing link between top predators and their environment.

In this thesis we demonstrated how specific environmental features influenced the foraging behaviour of Weddell seals. These habitat characteristics are likely to influence the distribution, availability and accessibility of prey in the environment at different spatial and temporal scales (Fauchald & Tveraa 2006). Weddell seals are expected to use these environmental cues to find areas associated with predictable prey patches, but also to adjust their behaviour according to the direct perception of prey in the water column. For instance, previous experience of prey encounter and/or depletion would influence their decision to stay and/or leave a given area according to the patch quality (Thums *et al.* 2013). Even though we attempted to develop the best proxies of foraging activity, the lack of data on prey distribution and availability on the East Antarctic shelf during winter, as well as the absence of concurrent information on prey encounters, prevented us from fully understanding how environmental parameters affected the focal Weddell seals.

Recently, head mounted accelerometers have proven to be efficient in detecting prey capture attempts in pinnipeds and penguins (Viviant *et al.* 2009; Watanabe & Takahashi 2013a). However, the use of these loggers in free-ranging animals have been hampered by the necessity to retrieve the tags to access the data. Recently, a new generation of head-mounted, miniaturized bio-logging devices have been developed and would help to address the central questions including (i) when and where predators encounter their prey; and (ii) what prey acquisition strategies are adopted according to the 3-D distribution of prey. Indeed, the novel satellite-relayed-3 axis accelerometer tags that directly process

the acceleration data on board before sending the data via Argos (SPLASH10-X tags, Wildlife Computers), providing the number of PrCA for each dive (C. Guinet, unpublished data). This ensures data collection from animals when the probability of tag retrieval is low, such as for Weddell seal deployments. In addition to providing information on prey encounters, these tags would allow estimates of diving and prey-pursuing energetic costs, by measuring data on stroke frequency. This information would vastly improve our understanding of the strategies adopted by Weddell seals that allow them to optimize their foraging behaviour.

3.2 Improving our understanding of climate variability effects on Weddell seals

3.2.1 Recent changes in sea-ice conditions in the DDU area

Based on the acclimation abilities of Weddell seals to extreme climatic events (see Chambert et al. 2012) and their behavioural plasticity observed in this thesis, we suggested Weddell seals would be more robust against climatic changes compared to other species (e.g. Adélie and emperor penguins). However, the population projections made by (Siniff et al. 2008; Chambert et al. 2012) predict that long-term changes of sea-ice conditions (predicted by climate change models) would be detrimental to Weddell seal populations. While much of East Antarctica has shown marginal changes in sea-ice seasonality since 1979 (Massom et al. 2013), the recent calving of the Mertz Glacier Tongue in 2010 has already affected sea-ice production and polynya activity in the area (Tamura et al. 2012, Dragon et al. 2014). Subsequent Adélie penguin breeding success at DDU has been poor in the last two years (Raymond et al. 2014). These observations show the urgency to conduct more ecological studies on Weddell seals in the East-Antarctic region and to

combine them with demographical studies to assess the impact of this abrupt event on focal Weddell seals. In addition, integrated ecological-demographical studies are needed to understand how winter habitat use and foraging strategies of Weddell seals affect their reproductive success.

3.2.2 Further investigation of sea-ice influence and pluri-regional studies are needed

A total of 32 seals from two different locations of East-Antarctica associated with contrasting sea-ice conditions and different topographic features were included in our analyses. Moreover, the studies were conducted on pluri-annual datasets. At both sites the foraging behaviour of Weddell seals was influenced by the bathymetric features, light intensity and the advance of winter. For most years the trends between their behaviour and these aspects of the environment were similar. However, despite similar foraging strategies and habitat usage observed between and within focal sites, our results also demonstrated high inter-individual variability. While this behavioural plasticity could be an important trait that allows Weddell seals to acclimate to extreme climatic events, it also shows the difficulty of assessing the impact of climate change on Weddell seals.

The trends observed in this thesis (*e.g.* focal Weddell seal behaviour versus topography, light intensity, advance of winter and associated darkness, and cold and thicker ice) are expected to be similar in other regions of Antarctica. On the other hand, we did not find that sea-ice features strongly influenced Weddell seal behaviour. However, our results showing that Weddell seals spend more time in areas likely associated with predictable ice cracks, compared with the projections made by other studies (Siniff *et al.* 2008; Massom & Stammerjohn 2010; Chambert *et al.* 2012), suggest that the influence of sea-ice on

Weddell seal foraging strategies needs to be investigated further. First, it is possible to acquire satellite images with a resolution high enough to detect small scale features in the fast-ice, such as tide cracks and small areas of open water. For instance, LaRue *et al.* (2011) demonstrated that using satellite images at 60 m resolution allowed an accurate count of Weddell seals and the detection of sea-ice features such as pressure ridges. However, in winter the acquisition of such images is not possible because of cloud coverage and darkness. Alternatively, the use of infrared high-resolution images (~1km) from sources such as the MODIS satellite (NASA, USA) could already provide valuable information. Second, we need to conduct similar studies at several regional sites around Antarctica in order to assess the influence of sea-ice dynamics in different regions on Weddell seals at a species level.

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APPENDIX

Appendix A

Chapitre du livre *Atlas des mammifères marins de France et d'Outre Mer* (sous presse), Service du Patrimoine Naturel, Muséum National d'histoire Naturelle, Paris

Le phoque de Weddell

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Appendix B – Script S2.1 of Paper 2

```
#########################################################
#####                                                   #####
#####              Hunting time method                  #####
#####  Optimised automated Broken stick algorithm  #####
#####                                                   #####
#########################################################

## Karine Heerah - February 2014
## A new method to quantify within dive foraging behaviour in marine
predators - K. Heerah, M. Hindell, C. Guinet, J-B, charrassin
## karine.heerah@hotmail.fr
## LOCEAN - UMR 7159, CNRS/UPMC/IRD/MNHN, 4 place Jussieu 75252 Paris
Cedex 05, France.

rm(list=ls())

data_path = "G:\\documents\\Weddell_seals\\data_TDR\\data\\" # path where
your TDR files are stored (after ZOC)
fig_path="G:\\documents\\Weddell_seals\\article_2\\script\\figure\\"   #
path for figures to be stored

setwd(data_path)

load("WED_08_samp.RData") ## load TDR files
dt$daytime <- as.POSIXct(dt$daytime,format="%d-%m-%Y %H:%M:%S",tz="GMT")
## Your dates need to be in

## POSIXct format
## column names: date-hour = "daytime", id = "seal", depth = "depth",
dive number = "num", temperature = "temp",
## ambient light = "light" etc.
## The only variables needed for the algorithm are: daytime, depth and
dive number. All the others are optionnal

dt <- dt[,c(1,2,5)] ## We only keep "daytime", "depth" and "num" columns.

#-----------------------------------------------------------------------
-----------------------------------------------------------------

##### Optimised Broken Stick Algorithm

# 1. Creation of output dataframes

d_env <- dt ## put your dataframe in the d_env variable which is used
troughout the script

num = unique(d_env$num) ## number of dives you have
num.list <- num


dbs                    <-                    data.frame("num"=rep(0,1),
"all.dur"=0,"start"=0,"end"=0,"depth_start"=0,"depth_end"=0,"seg"=0,"npo
ints"=0,
```

```
      "dur"=0,"dur.per"=0,"coef"=0,
"mean_depth"=0,"max.depth"=0,"sinuosity"=0,"mean_err"=0,"foraging"=0) ##
Broken stick dataframe

## num = dive number, all.dur = total dive duration, start = date of
segment start, end = date of segment start,
## depth_start = depth of segment start, seg = broken stick segment number,
npoints = number of points summarising the dive
## dur = duration of each segment, dur.per = % of total duration, coef =
slope coefficient of the segment,
## mean_depth = mean depth of segment, max.depth = maximum dive depth,
sinuosity = vertical sinuosity associated to this part of the dive,
## mean_err = mean distance between original dive profile and the
reconstructed one for the optimal number of broken stick points,
## foraging = behaviour according to vertical sinuosity threshold

ncdv = data.frame("daytime"=rep(0,1) ,"depth"=0,"num"=0) ## dataframe in
which the dives for which the fit doesn't work will be stored.
                                                          ##   Needs   to
have a same column names exactly

#-------------------------------------------------------------------------
-------------------------------------------------------------------
# loop for each dive

for(d in 1:length(num.list)){
  print(d)
  dt <- d_env[d_env$num==num.list[d],]
  if(nrow(dt) > 60 ) {  ##consider dives of more than 60s as the resolution
of the dataset is 1s
    ndive=num.list[d]

    #plot(as.numeric(dt$daytime),   dt$depth,   ylim=c(max(dt$depth),0),
t="l", ylab="depth (m)", xlab="",xaxt="n")
    #Use only if you want to check your dive
    #axis.POSIXct(1,x=dt$daytime,     format="%H:%M:%S",     labels     =
TRUE,cex.lab=0.5)
    #idem

    np <- c(3:30)   ## number of broken stick iterations to see which
optimal number of points summarise your dive
    npe=rep(NA,28) ## vector where the average distance between original
and reconstructed dive profile is stored
    npo=rep(NA,28) ## vector where the number of broken stick points
describing the dive profile is stored


### Finding the optimal number of Broken points for each dive

# 1.Loop to define the mean distance depending on the number of broken
stick points

  for (k in 1:length(np)){
      npp = np[k] # selection of the number of iteration: from 3 to 30
      # 2 lines below: selection of the depth and time for the 2 surface
points and the maximum depth point
      ref <- c(dt$depth[1],max(dt$depth),dt$depth[nrow(dt)])
      tim                                                          <-
c(as.numeric(dt$daytime[1]),as.numeric(dt$daytime[dt$depth==max(dt$depth
)][1]),as.numeric(dt$daytime[nrow(dt)]))
```

```
      for (i in 1:npp){
        #plot(as.numeric(dt$daytime), dt$depth, ylim=c(max(dt$depth),0),
t="l", ylab="depth (m)", xlab="",xaxt="n")
        # plot only if you want to see how the broken stick algorithm is
working
        #points(tim,ref, pch=19, cex=1, col="red")
        #idem
        interp     <-     approx(tim,ref,xout=dt$daytime,method="linear")
#linear interpolation between broken stick points at TDR time interval
        #lines(interp,col="red")
        #idem
        dif_x <- as.numeric(interp$x - dt$daytime) # time differences
between original and reconstructed profiles
        dif_y <- interp$y - dt$depth # depth differences between original
and reconstructed profiles
        dst <- sqrt(dif_x^2 + dif_y^2) # calculate distances between
original and reconstructed profiles

        ii <- which(dst==max(dst))[1] # index of the data point of maximum
difference between original and reconstructed profiles
        #points(dt$daytime[ii],dt$depth[ii],col="blue",pch=19,cex=1)
        #idem
        tim <- c(as.numeric(tim),as.numeric(dt$daytime[ii])) # add new
broken stick point time
        tim <- ISOdatetime(1970,1,1, 0,0,0, tz="gmt") + tim
        ref <- c(ref,dt$depth[ii]) # add new broken stick point depth
      }
      npe[k] = mean(dst) # average distance between original and
reconstructed dive profiles
      npo[k] = length(tim) # number of broken stick points describing the
dive profile
    }


# 2. Defining the optimal number of broken stick points

    f <- data.frame(npe=npe, npo=npo)
    #plot(f$npo, f$npe,xlab="nb of points", ylab="mean error") #plot of
mean distance between original and reconstructed dive profiles
                                                                #
according to the number of broken stick points describing the dive
                                                                #activate
only if you want to check

    # Use of a gompertz model to find the curve which best fit our data
    Asym <- 0; b2 <- -5; b3 <- 0.9
    fm1 <- -999
    try(fm1 <- nls(npe ~ SSgompertz(npo, Asym, b2, b3), data=f,
control=nls.control(maxiter=500)),TRUE) #gompertz model to fit an
asymptote
    #curve to the mean distance between original and reconstructed dive
profiles plot

    if (class(fm1) == "nls"){ # if the model converged, we can go to the
next steps
      #summary(fm1)
      tt <-predict(fm1, f$npe)


      # plot of the mean distance
```

```
png(paste(fig_path,"WED_BS_",ndive,"_",substr(dt$daytime[1],1,10),".png"
, sep=""),pointsize=12*1.5,height=480*1.5,width=480*1.5)

      par(mfrow=c(2,1),mar=c(4,4,2,2))
      tit=paste("BS_WED08_",ndive,"_",substr(dt$daytime[1],1,10))
      plot(f$npo, f$npe,xlab="nb of points", ylab="mean error",main=tit)
      lines(na.omit(f$npo),tt[1:28],col="red")

      # Plot the linear approximation between the first and last point of
the fitted curve
      t   <-   data.frame(npe=c(f$npe[1],   f$npe[28]),   npo=c(f$npo[1],
f$npo[28]))
      interp      <-      approx(c(f$npo[1],f$npo[28]),c(tt[1],tt[28]),
xout=f$npo,method="linear")
      interp$x <- interp$x[!is.na(interp$x)]
      interp$y <- interp$y[!is.na(interp$y)]
      lines(interp$x, interp$y,col="blue")

      # Looking for the inflexion point which is the furthest point
between the fitted curve and the approximation
      dif_x <- interp$x - na.omit(f$npo)
      dif_y <- interp$y - tt[1:28]
      dst <- sqrt(dif_x^2 + dif_y^2)
      dm <- f$npo[which(dst==max(dst))]

      points(f$npo[which(dst==max(dst))],   f$npe[which(dst==max(dst))],
pch=19, col="red") ## inflexion point


#3. optimal broken stick method for each dive

      # The two lines below select the optimal number of broken stick
points (in their order of appearance in the BS iteration)
      # example: surface start point, max. depth point, surface end point
+ x other points
      tim= tim[1:dm]
      ref=ref[1:dm]

      tim2 <- sort(tim)
      dep_tim <- as.data.frame(cbind(ref,tim))
      dep_tim <- dep_tim[order(tim),]

      dbs2      <-      data.frame("num"=rep(0,(nrow(dep_tim)-1))      ,
"all.dur"=0,"start"=0,"end"=0,"depth_start"=0,"depth_end"=0,"seg"=0,"npo
ints"=0,          "dur"=0,"dur.per"=0,"coef"=0,          "mean_depth"=0,
"max.depth"=0,"sinuosity"=0,"mean_err"=0)

      # Loop to calculate the different metrics for each broken stick
segments
      for (n in 1:(nrow(dep_tim)-1)){
        x1= dep_tim$tim[n] # start of BS segment
        x2= dep_tim$tim[n+1] #end of BS segment
        dbs2$num[n]=ndive
        dbs2$all.dur[n]=difftime(dt$daytime[nrow(dt)],    dt$daytime[1],
tz,units = c("secs")) #dive duration
        dbs2$start[n]=x1
        dbs2$end[n]=x2
        dbs2$depth_start[n]= dep_tim$ref[n] # depth of start of BS segment
        dbs2$depth_end[n]= dep_tim$ref[n+1] # depth of end of BS segment
        dbs2$seg[n]=n #segment number
```

```
        dbs2$npoints[n]=nrow(dep_tim) # optimal BS points summarising the
original dive profile
        dbs2$dur[n]= difftime(tim2[n+1], tim2[n], tz,units = c("secs"))
#duration of the segment in sec.
        dbs2$dur.per[n]=(dbs2$dur[n]/dbs2$all.dur[n])*100 #% of segment
duration according to total dive duration
        dbs2$coef[n]=(dep_tim$ref[n+1]  -  dep_tim$ref[n])/(x2  -  x1)  #
slope coefficient of the segment

dbs2$mean_depth[n]=mean(dt$depth[which(as.numeric(dt$daytime)==x1):which
(as.numeric(dt$daytime)==x2)]) #mean depth of the segment
        # calculated from original profile depths
        dbs2$max.depth[n]= max(dt$depth) # dive max. depth

        #Calculation of vertical sinuosity
        deuc= abs(dep_tim$ref[n+1] - dep_tim$ref[n]) # Vertical distance
swum between 2 BS points

dobs=sum(abs(diff(dt$depth[which(dt$daytime==x1):which(dt$daytime==x2)])
)) # sum of all the vertical distances from the original
        #profile between the two corresponding BS depth points

        dbs2$sinuosity[n]=deuc/dobs # vertical sinuosity index
        dbs2$mean_err[n]=f$npe[which(dst==max(dst))]  #  mean  distance
between original and reconstructed dive profiles for the optimal
        #number of BS points summarising the dive.
      }

      #-----------------------------------------------------------------
-----------------------------------------------------------------
      # IMPORTANT:
      #-----------
      # Attribution of behaviour according to vertical sinuosity -- Remind
that the sinuosity threshold used here was determined according
      # to the histogram/density plot of vertical sinuosity for every BS
segments of every dive
      # so, before setting your threshold at 0.9, check if it suits your
dataset (i.e after running the BS on all your dives)

      dbs2$foraging <- 2 ## 2 stands for "hunting" mode
      dbs2$foraging[dbs2$sinuosity >=0.9 & dbs2$sinuosity <=1] <-1 ## 1
stands for "transit" mode
      #-----------------------------------------------------------------
-----------------------------------------------------------------

      # Dive plot: original dive profile and Broken stick reconstructed
profile
      sg <- unique(dbs2$seg)
      cl <- c("blue","red")
      dbs2$code[dbs2$sinuosity]

      plot(as.numeric(dt$daytime),                                dt$depth,
ylim=c(max(dt$depth),0),t="l",ylab="depth (m)", xlab="",xaxt="n")
      points(tim,ref, pch=19, cex=1, col="black")
      lines(approx(tim,ref,xout=dt$daytime,method="linear"),col="black")
      for(i in 1:length(sg)){

lines(c(dbs2$start[dbs2$seg==sg[i]],dbs2$end[dbs2$seg==sg[i]]),c(dbs2$de
pth_start[dbs2$seg==sg[i]],
```

```
dbs2$depth_end[dbs2$seg==sg[i]]),col=cl[dbs2$foraging][dbs2$seg==sg[i]],
lwd=2.5)
        }
      axis.POSIXct(1,x=dt$daytime,       format="%H:%M:%S",labels       =
TRUE,cex.lab=0.5)
      dev.off()
      dbs <-rbind(dbs,dbs2)
    } else {ncdv<-rbind(ncdv,dt)} # allows to keep somewhere the data for
which the fit of the Gompertz model didn't work ,
  } #end of if loop for 60 s
  #save(dbs, file="BS_fitmet_WED_08_samp.RData")
} #end of for loop for dive number

dbs<- dbs[-1,]

hist(dbs$sinuosity,xlab="sinuosity",breaks=seq(0,1,0.1),main="")  ##  See
line 191
abline(v=0.9,col="red",lwd=2)

ncdv <- ncdv[-1,]
#save(ncdv, file="BS_err_WED_08_samp.RData")
#save(dbs, file="BS_fitmet_WED_08_samp.RData")
```